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Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

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Editor's Foreword

The *Journal*, whose origin dates back to 1901, expanded its scope in 1971, to include special issues on proceedings of major international conferences and on significant series of papers on broad topics with relevance to aquatic science in Canada.

The first conference proceedings appeared in 1972 (Vol. 29, No. 6) on Salmonid Communities in Oligotrophic Lakes (SCOL). Five years and 11 special issues later, we present here the proceedings of SCOL's close relative — the Percid International Symposium (PERCIS).

In February 1974 at a meeting of scientists and managers of the Ontario Ministry of Natural Resources, convened by Mr Kenneth H. Loftus, the decision was made to organize an international conference on percid communities. Its basis was to be the concern for the welfare of percid stocks and the need for basic information on community ecology for management purposes.

PERCIS followed the SCOL model. It was held over a 12-day period from September 24 to October 5, 1976 in the relaxed surroundings of the Quetico Centre in the wilds of Northwestern Ontario. Papers were supplied in advance and were exposed to in-depth discussion and criticism, and revisions were made following the symposium.

The success of PERCIS, as attested by its proceedings contained in this issue, must be attributed to the 70 scientists from 12 countries who participated. But the person who spearheaded PERCIS and saw it through from beginning to end was Dr Peter J. Colby. He organized it, chaired the Symposium, and acted as Special Editor of the proceedings with the able assistance of Mr R. H. Wigmore. PERCIS was a labor of love for Dr Colby, for which all readers of this issue will be grateful.

The *Journal* is privileged to publish these proceedings, which significantly advance world knowledge on percid fishes.

J. C. STEVENSON
Editor and Director of
Scientific Information

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Note du directeur

Le *Journal*, dont l'origine remonte à 1901, a élargi son mandat en 1971: il publie maintenant des numéros spéciaux où sont reproduits les comptes rendus de conférences internationales et des séries d'articles d'importance sur des sujets généraux se rapportant à la science aquatique au Canada.

Les premiers comptes rendus, ceux du colloque sur les communautés de salmonidés dans les lacs oligotrophes (SCOL), parurent en 1972. Cinq ans et 11 numéros spéciaux plus tard, nous présentons aujourd'hui les comptes rendus d'un proche parent de SCOL, ceux du colloque international sur les percidés (PERCIS).

En février 1974, M. Kenneth H. Loftus convoquait une réunion des scientifiques et des gestionnaires de l'Ontario Ministry of Natural Resources, où il fut décidé d'organiser une conférence internationale sur les communautés de percidés. La conférence porterait sur la protection des stocks de percidés et sur le besoin, pour la gestion, de connaissances de base sur l'écologie des communautés.

PERCIS adopta le format de SCOL. La conférence a duré 12 jours, soit du 24 septembre au 5 octobre 1976, dans le milieu reposant qu'est le Centre Quetico dans la région sauvage du nord-ouest de l'Ontario. Les articles, préparés à l'avance, furent l'objet de discussions et de critiques en profondeur et furent révisés après le colloque.

On doit attribuer aux participants, 70 scientifiques provenant de 12 pays, le succès de PERCIS, comme le démontrent les comptes rendus que contient le présent numéro. Mais M. Peter J. Colby fut l'âme dirigeante du colloque, du commencement à la fin. Il l'organisa, présida le colloque lui-même et agit comme éditeur spécial des comptes rendus, avec l'aide compétente de M. R. H. Wigmore. M. Colby s'est consacré à PERCIS avec plaisir, et tous les lecteurs de ce numéro lui en seront reconnaissants.

C'est un privilège pour le *Journal* de publier ces comptes rendus qui représentent un progrès marqué des connaissances, à l'échelle mondiale, sur les percidés.

J. C. STEVENSON
Directeur de la publication
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Introduction to the Proceedings of the 1976 Percid International Symposium (PERCIS)[1,2]

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THE Symposium evolved from two needs: First to summarize information as a basis for management of percid fish communities in the shallower waters of the Laurentian Great Lakes and in other lakes; and secondly to provide a sequel and extension of the SCOL symposium methodology (J. Fish. Res. Board Can., Vol. 29, No. 6) which has focused on salmonid communities in the northern hemisphere and explored their responses to alternate uses of aquatic resources, employing existing information to develop relevant inferences. With the conviction that these needs were real and that appropriate information existed, PERCIS was held at Quetico Centre, Ontario, from September 24 to October 5, 1976.

Content

The proceedings of the Symposium are the most comprehensive collection of papers on the biology and ecology of the more economically important members of the family Percidae assembled to date. The proceedings present a balance of fact and theory for the benefit of researchers, resource managers, and informed laymen. The reader will find an exceptional compilation of long-term data series showing changes in various fish communities with time. Also presented are numerous innovative and conceptually stimulating hypotheses and models relevant to contemporary management needs.

PERCIS has focused on improved descriptions of percid habitats and compilation of information which permits a prediction of community changes resulting from habitat modification, exploitation, and other cultural disturbances.

The contributions from Europe introduce the reader to or further inform him of the implications of functional morphology, the value of the guild concept in predicting community changes and species succession when habitat is altered, new methodology for estimating age compositions of fish populations, advantages of precise knowledge of fishing effort in making management decisions, and a description of percid habitats in eastern Europe.

Approach

PERCIS was organized as a workshop-type symposium. Seventy committed researchers from 12 countries drew inferences from previously compiled information in an informal atmosphere. Although certain data by themselves were considered limited in value, collectively the information permitted generalizations to be made concerning the biology, dynamics, habitat requirements, and environmental tolerances of percid communities (fish communities containing percids), their comparisons, contrasts, and possible interaction with other fish communities (i.e. coldwater salmonid communities and warmwater centrarchid communities) and man.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Contribution No. 77-4 of the Ontario Ministry of Natural Resources, Fish and Wildlife Research Branch, Maple, Ont.

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Compilation, assimilation, and synthesis of data were accomplished in three phases. First, background papers describing the biology, community characteristics, and habitat requirements of percids were prepared and distributed to participants well in advance of the symposium. These papers provided background information on ecological significance of body form and function, physiological tolerance, and behavioral characteristics of various fishes to better understand and predict how a fish community will respond to a changing environment. Phase two involved the preparation of lake case-histories for the purpose of compiling organized blocks of data from long-term studies to evaluate trend-in-time changes in populations and communities and their responses to cultural disturbances. Past habitat modifications and management practices were reviewed as stimulus–response experiments using fish communities not with the intent of evaluating the modifications or practices, but rather to compare and contrast various community responses to known stimuli.

Phase three involved synthesizing material contained in background and case-history papers and formulating inferences (preparing synthesis and inference papers) immediately before and during the symposium. Insights into the dynamics and properties of populations and communities were sought by examining the next hierarchical level, community, and the ecosystem, respectively.

Resolution — During the process of developing meaningful generalizations certain constraints on conjecture had to be resolved; a balance between reaching for the truth and losing credibility had to be gained.

T. H. Huxley explained years ago: "... anyone who is practically acquainted with scientific work is aware that those who refuse to go beyond fact, rarely get as far as fact; and anyone who has studied the history of science knows that almost every great step therein has been made by ... the invention of hypothesis, which, though verifiable, often has very little foundation to start with; and, not infrequently, in spite of a long career of usefulness, turned out to be wholly erroneous in the long run."

In these proceedings we reached for facts through extrapolation and speculation but required a reasonable amount of supporting evidence to retain credibility. Much of the material because of its conjectural nature (especially in inference papers) would probably be published in "Perspectives" in a regular issue of this Journal, and the reader should weigh the value of the concepts in light of the supporting evidence. However, one of our primary objectives was to generate ideas and concepts by encouraging free expression and dialogue fortified with available supporting evidence. Where evidence was weak or lacking, we asked that sufficient qualifications be given.

The participants in the symposium have no illusions that all possible syntheses and inferences have found their way into the proceedings. We hope other contributions from PERCIS will be forthcoming in time.

A general outline of PERCIS program follows:

BIOLOGY OF PERCIDS (background papers)
  Evolution and Systematics
  Morphology, Physiology, and Behavior
  Population Dynamics, Plasticity, and Ecology

PERCID HABITAT (background papers)
  Lake Classification
  Habitat
  Productivity

COMMUNITY DYNAMICS AND INTERACTIONS
  Spatial (inshore and offshore)
  Temporal
  Trophic
  Biological Interactions

INTERACTIONS WITH MAN (case history papers)
  Little Influence by Man
  Habitat Modification
  Population Structuring
  Community Structuring

MODELS AND INFERENCES

Acknowledgments

I acknowledge the energy expended by the participants in preparing their contributions to the proceedings, their sharing of insights and criticisms, and their roles in expanding significantly our knowledge of percid fishes. I am especially indebted to members of the steering committee: C. A. Elsey of Canada, J. Holčik of Czechoslovakia, M. G. Johnson of Canada, J. H. Leach of Canada, J. J. Magnuson of U.S.A., C. H. Olver of Canada, and J. E. Thorpe of Scotland. The committee formulated the program, chose the participants to be invited, and shared in editorial responsibilities. Others sharing in organizing, editing, or reviewing manuscripts, or promoting PERCIS were, P. H. Eschmeyer of the U.S.A. and F. E. J. Fry, A. H. Lawrie, N. V. Martin, H. A. Regier, J. D. Roseborough, and R. A. Ryder of Canada.

Assistance with secretarial duties provided by Barbara Pike, Betty Wilkinson, and Roma Hamilton and with arrangements by Terry Marshall, Tom Mosindy, and Brian Renaud was appreciated by everyone.

Financial support for the symposium came from the Great Lakes Fishery Commission, the International Joint Commission, the Fisheries and Marine Service of Fisheries and Environment Canada, the Toronto Sportsmen Show, the Manitoba Department of Renewable Resources and Transportation Services, and the Ontario Ministry of Natural Resources.

Finally, with special gratitude, I acknowledge the help of K. H. Loftus and R. H. Wigmore whose respective promotional and editorial abilities made PERCIS both possible and readable.

Systematics and Zoogeography of the Fishes of the Family Percidae[1]

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COLLETTE, B. B., AND P. BĂNĂRESCU. 1977. Systematics and zoogeography of the fishes of the family Percidae. J. Fish. Res. Board Can. 34: 1450–1463.

Two phyletic lines are present in the Percidae: the Percinae, in which the anteriormost interhaemal bone is much larger than the posterior ones and the anal spines usually are well developed, and the Luciopercinae, in which the interhaemal bones are of uniform size and the anal spines are poorly developed. Parallel evolution has produced in each subfamily small, benthic, rheophilic forms with depressed or terete bodies and reduced or vestigial swimbladders. This differentiation is shown by dividing each subfamily into two tribes. Within the Percinae, the Etheostomatini (*Percina*, *Ammocrypta*, and *Etheostoma*) are interpreted as derivatives of the Percini (*Perca*, *Gymnocephalus* [=*Acerina*], and *Percarina*). The North American species *Perca flavescens* is distinguished from the Eurasian species *P. fluviatilis* and *P. schrenki* on the basis of the more posterior position of the predorsal bone. In the Luciopercinae, the Romanichthyini (*Zingel* [=*Aspro*] and *Romanichthys*) have evolved from the Luciopercini (*Stizostedion* [including *Lucioperca*]).

Key words: Percidae, systematics, zoogeography, evolution

COLLETTE, B. B., AND P. BĂNĂRESCU. 1977. Systematics and zoogeography of the fishes of the family Percidae. J. Fish. Res. Board Can. 34: 1450–1463.

Il existe chez les Percidae deux lignées phylétiques: les Percinae, chez lesquels l'os interhémal le plus avant est beaucoup plus gros que l'os postérieur, et les épines anales sont ordinairement bien développées, et les Luciopercinae, chez lesquels les os interhémaux sont de grosseur uniforme et les épines anales faiblement développées. Une évolution parallèle a produit dans chaque sous-famille de petites formes rhéophiles benthiques à corps déprimé ou térétiforme et à vessie gazeuse réduite ou vestigiale. La séparation de chaque sous-famille en deux tribus reflète cette différenciation. Parmi les Percinae, on considère les Etheostomatini (*Percina*, *Ammocrypta* et *Etheostoma*) comme dérivés des Percini (*Perca*, *Gymnocephalus* [=*Acerina*] et *Percarina*). L'espèce nord-américaine *Perca flavescens* se distingue des espèces eurasiennes *P. fluviatilis* et *P. schrenki* par la position plus arrière de l'os prédorsal. Chez les Luciopercinae, les Romanichthyini (*Zingel* [=*Aspro*] et *Romanichthys*) ont évolué à partir des Luciopercini (*Stizostedion* [y compris *Lucioperca*]).

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THE purpose of this paper is to review the systematics, morphology, and distribution of the Percidae. The family, subfamilies, and tribes are defined based largely on an earlier paper (Collette 1963). Complete generic synonymies are presented to help stabilize the nomenclature of the family at the generic level. For the most speciose tribe, the North American Etheostomatini, the generic (and subgeneric) treatment follows Bailey and Gosline (1955), Collette (1965), Collette and Knapp (1967), and Page (1974). Information on the family in general, but particularly on the European species, has come from Chevey (1925), Berg (1949), and Bănărescu (1964). Additional research is needed to define the subgenera of *Etheostoma* and to describe about 25–30 undescribed species of *Etheostoma* and *Percina*; otherwise, the classification of the Percidae appears to be reasonably stable.

Characteristics of Percid Taxa

Following are definitions of the family, and of the subfamilies and tribes that we recognize within the Recent Percidae. The relationships

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[1] This paper forms part of the proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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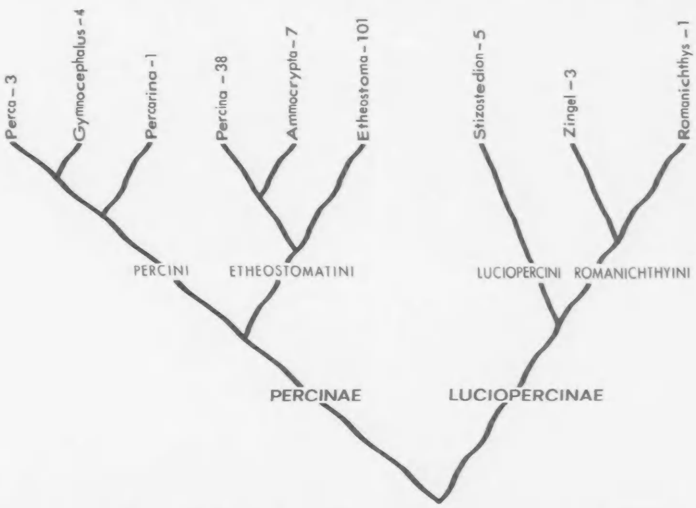

FIG. 1. Relationships of the subfamilies, tribes, and genera of the Percidae. *Number of species indicated for each genus.*

between the suprageneric categories are outlined in Fig. 1. The characteristics of the family are based on Collette (1963) which was modified from Regan (1913) and Berg (1955), and supplemented by characters from Gosline (1966a, b) and Johnson (1975).

PERCIDAE

Percoid fishes generally similar to other families of basal percoids in having the spinous dorsal fin well developed; the pelvic fins thoracic, with one spine and five branched rays; two nostrils on each side of the head; preopercle serrate except in many Etheostomatini; five to eight branchiostegal rays; four gills, a slit behind the fourth; brancheostegal membranes free from isthmus; supramaxillary absent; villiform or cardiform teeth on upper and lower jaws; teeth present on vomer and palatines except in some specialized Etheostomatini; no scaly process in axil of pelvic fin (Gosline 1966b); epipleural ribs starting on the first vertebra, pleural ribs starting on the third; no spur on posteriormost procurrent ray of caudal fin and preceding procurrent ray not basally shortened (Johnson 1975); caudal skeleton with three epurals; branched caudal rays usually 8 + 7, principal caudal rays usually 9 + 8, procurrent caudal rays (10–15) + (8–13). Similar to the Centrarchidae and Cichlidae and different from the Serranidae and many other marine percoids in lacking a subocular shelf and having one or two instead of three anal spines. Different from Percichthyidae and several other basal percoid families in lacking the procurrent spur (Johnson 1975). Different from most percoid families in having one or no predorsal bone (auxiliary interneural) instead of two or more; predorsal bone extending anterior to first neural spine or between first and second neural spines. Vertebrae 32 to 50. Freshwater fishes of the northern hemisphere.

PERCINAE

Percidae with the anteriormost interhaemal bone greatly enlarged; anal spines usually large and well developed; lateral line usually not extending onto caudal fin, and supplementary lateral lines on caudal fin absent except sometimes in *Gymnocephalus schraetser*.

Percini Bonaparte, 1831

Percinae reaching moderate size; supraoccipital crest well developed; predorsal bone present except in *Percarina*; branchiostegal rays usually 7 or 8; preopercle strongly serrate; genital papilla small or absent; body compressed; anal spines very prominent; swimbladder well developed; breeding tubercles absent; vertebrae 33–43. Three genera: *Perca* Linnaeus (3 species), *Gymnocephalus* Bloch (4 species), and *Percarina* Nordmann (1 species) found in Eurasia and North America.

Perca Linnaeus

Perca Linnaeus 1758: 289. Type-species *Perca fluviatilis* Linnaeus by subsequent designation of Gill (1861a: 48). Placed on the Official List of Generic Names by Opinion 77, Int. Comm. Zool. Nomencl.).

Epitrachys Schulze 1889: 209. Type-species *Perca fluviatilis* Linnaeus by original designation.

Eoperca Jordan 1919a: 12. Type-species *Mioplosus multidentatus* Cope (= *Perca flavescens* Mitchill) by original designation.

Perca fluviatilis Linnaeus is widespread throughout Europe and Asia (Fig. 2). In Europe, the highlands of Scotland and Norway limit its northern distribution and the Pyrenees have prevented it from entering the Iberian Peninsula (Weatherley 1963). It is present in the Baltic Sea basin, throughout the Gulf of Finland, the White Sea basin, and the Arctic Ocean basin from the Kola to the Kolyma, but is absent from the Amur. Fossil *P. fluviatilis* have been found farther eastward, in the Kyrchak Peninsula (Lebedev 1960) in Quaternary deposits. *Perca fluviatilis* has been introduced into many other parts of the world (Thorpe 1977, fig. 1): South Africa; Tasmania, Victoria, and New South Wales, Australia; and New Zealand. It is replaced by *P. flavescens* (Mitchill) in eastern North America natively from Labrador to Georgia and east to the Mississippi. *Perca flavescens* has been introduced south and west of its original range in the United States (Weatherley 1963).

Svetovidov and Dorofeeva (1963) considered the Eurasian and North American yellow perches to be conspecific. They described the population of *P. fluviatilis* in the Kolyma River basin of northeastern Siberia as *P. f. intermedius* because they considered it to be intermediate between the European subspecies *P. fluviatilis fluviatilis* and the North American subspecies *P. fluviatilis flavescens*. After reviewing the published morphological data and comparing biological characteristics such as time of and temperature at spawning, fecundity, and growth, Thorpe (1977) concluded that there are no biological reasons to maintain *flavescens* and *fluviatilis* as separate species. We have recently found that the predorsal bone extends between the first and second neural spines in *P. flavescens* in contrast to anterior to the first neural spine in *P. fluviatilis* (Fig. 3). The pterygiophore supporting the first dorsal spine extends between the second and third neural spines in *P. flavescens*, but between the first and second neural spines in *P. fluviatilis*. This relationship was invariable in radiographs of over 120 *P. fluviatilis* and 65 *P. flavescens* from throughout their ranges. The predorsal bone in *Gymnocephalus* spp. is also anterior to the first neural spine, indicating that the posterior position in *P. flavescens* is a derived condition. We conclude that *P. flavescens* must be maintained as a valid species. Reeve M. Bailey and Gerald R. Smith have uncovered a number of additional characters

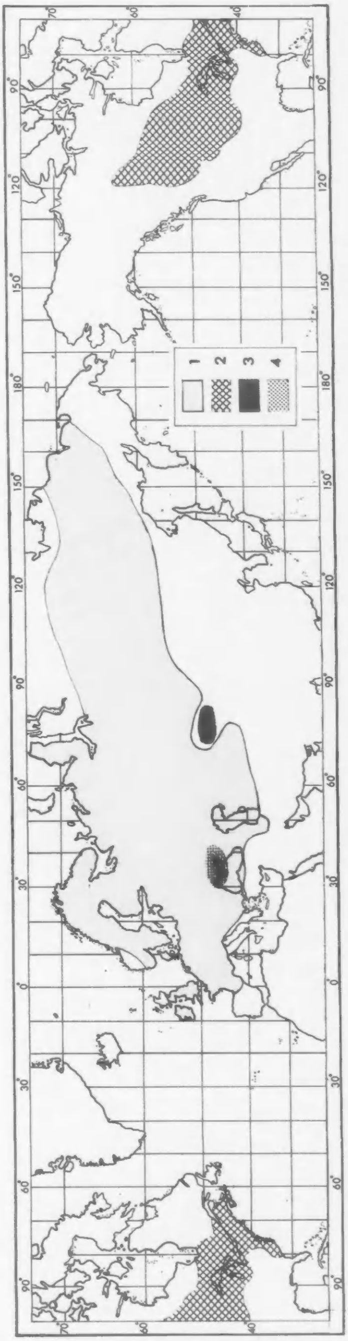

FIG. 2. Native distributions of the species of *Perca* and *Percarina*. (1) *Perca fluviatilis*; (2) *P. flavescens*; (3) *P. schrenki*; (4) *Percarina demidoffi*.

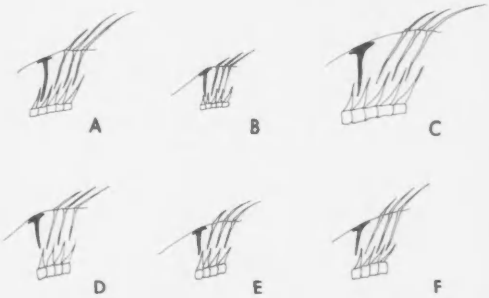

FIG. 3. Positions of predorsal bone (in solid black) relative to the neural spines of the first four vertebrae and the pterygiophores supporting the anterior three dorsal spines in the species of *Perca*. A–C, *P. flavescens*: (A) Wisconsin, USNM 7472; (B) Maryland, USNM 90480; (C) St. Lawrence River, USNM 49037. D–E, *P. fluviatilis*: (D) Volga River, USSR, USNM 62371; (E) Switzerland, USNM 12691; (F) *P. schrenki*, Ili River, Kazakhstan, USNM 37269.

that verify the validity of *P. flavescens* (R. M. Bailey personal communication).

The third species in the genus, *P. schrenki* Kessler, is confined to the Balkhash and Alakul' lakes system in the Asiatic highlands of eastern Kazakh S.S.R., allopatric but adjacent to the range of *P. fluviatilis*. *Perca schrenki* has the same predorsal bone arrangement as *P. fluviatilis*. Recent information on *P. schrenki* is presented by Berg (1949), Zhadin (1949), and Nikolsky and Evtyukhov (1940).

Gymnocephalus Bloch

Cernua Schaeffer 1761: 37. Type-species *Cernua seu perca fluviatilis minor* Schaeffer (= *Perca cernua* Linnaeus) by subsequent designation of Jordan 1917: 16. Invalid as a work that is not consistently binomial (Opinion 345, Int. Comm. Zool. Nomencl.).

Schraitzer Schaeffer 1761: 38. Type-species *Schraitser Ratisbonensium* Schaeffer (= *Perca Schraetzer* Linnaeus) by subsequent designation of Jordan 1917: 16. Invalid as a work that is not consistently binomial (Opinion 345, Int. Comm. Zool. Nomencl.).

Percis Klein *in* Walbaum 1792: 585. Type-species *Perca cernua* Linnaeus by subsequent designation of Bleeker 1876: 266. By reprinting the names of Klein (1774), Walbaum did not give them nomenclatural status (Opinion 21, Int. Comm. Zool. Nomencl.).

Gymnocephalus Bloch 1793: 24. Type-species *Perca schraetser* Linnaeus by subsequent designation of Bleeker 1876: 266.

Acerina Cuvier 1817: 283. Type-species *Perca cernua* Linnaeus by subsequent selection of Jordan 1917: 104.

Cernua Fleming 1828: 212. Type-species *Cernua fluviatilis* (= *Perca cernua* Linnaeus) by monotypy.

Leptoperca Gill 1861b: 502. Type-species *Perca schraetser* Linnaeus by original designation.

The species of *Gymnocephalus* are characterized by hypertrophy of the lateral line canals on the head (particularly the infraorbital and preoperculomandibular canals), presumably an adaptation to slow-moving, relatively turbid waters where vision cannot play such an important role as in clearer waters. Holčík and Hensel (1974) postulated a Paleodanube origin for *Gymnocephalus* and showed the distributions of the four species (Fig. 4). *Gymnocephalus cernuus* (Linnaeus) is the most widespread species, inhabiting north, central and eastern Europe, including northeastern France, England but not Scotland or Ireland, the rivers entering the Baltic Sea, the rivers entering the White sea, and all Siberia including the Kolyma River but excluding the Amur. *Gymnocephalus baloni* Holčík and Hensel is a Danube endemic. Both *G. cernuus* and *G. baloni* are primarily inhabitants of slow flowing waters of lowlands; both feed on small bottom invertebrates. *Gymnocephalus acerinus* (Güldenstadt) is found in the northern tributaries of the Black Sea — the Dniester, southern Bug, Dnieper, Don, Donets, and Kuban. *Gymnocephalus schraetser* (Linnaeus) is endemic to the Danube and Kamchia rivers. *Gymnacephalus schraetser* and *G. acerinus* live in running waters over sand or gravelly bottom. In addition to Holčík and Hensel (1974), other important references on the

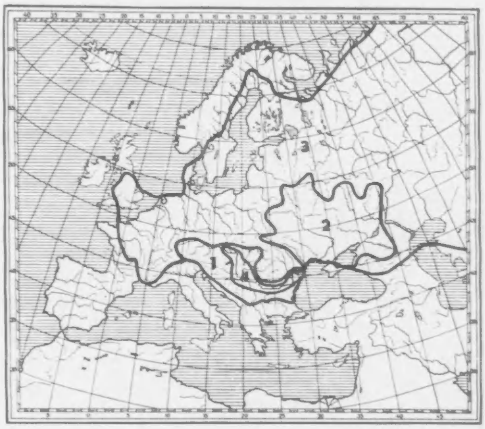

FIG. 4. Native distributions of the species of *Gymnocephalus* (from Holčík and Hensel 1974: fig. 11). (1) *G. schraetser*; (2) *G. acerina*; (3) *G. cernuus* (only part of its Asiatic distribution); (4) *G. baloni*.

morphology, distribution, and systematics of *Gymnocephalus* spp. include Mohr (1943), Oliva (1959), Safránek (1962), and Aleksandrova (1974).

Percarina Nordmann

Percarina Nordmann 1840, III: 357. Type-species *Percarina demidoffi* Nordmann by monotypy.

In association with a reduction in size, *Percarina* lacks the predorsal bone found in other Percini. *Percarina demidoffi* Nordmann is found in the northern, weakly saline portions of the Black Sea and the Sea of Azov (Fig. 2). Two subspecies are recognized by Berg (1949) and others: *P. d. demidoffi* in the Black Sea (estuaries of the Don, Dnieper, southern Bug, and Dneister) and *P. d. maeotica* Kuznetsov (northeastern and eastern parts of the Sea of Azov, in particular the Gulf of Taganrog, rarely in the mouths of the Don and Kuban). *Percarina d. maeotica* has a smaller eye than does *P. d. demidoffi* and has the head and prepectoral region covered with scales instead of naked (Kuznetsov 1887; Berg 1949).

Etheostomatini Agassiz 1850

Percinae reaching small to moderate size; supraoccipital crest greatly reduced; predorsal bone absent; branchiostegal rays usually 5 or 6; preopercle entire or partially serrate; genital papilla usually well developed in females; body slightly compressed or fusiform; anal spines usually moderately prominent; swimbladder reduced or absent; breeding tubercles present in males of some species of all genera; vertebrae 32–48. Three genera confined to North America (Fig. 5): *Percina* Haldeman (30 valid described species plus about 8 undescribed species, Jenkins 1976), *Ammocrypta* Jordan (7 species), and *Etheostoma* Rafinesque (84 valid described species plus about 17 undescribed species Jenkins 1976). This total of 146 species compares favorably with the curve extrapolated by Collette (1967) which predicted that 160 species and subspecies of Etheostomatini would be known by the year 2000.

The generic synonymies are based on the lists of available and unavailable genus-group names presented by Collette and Knapp (1967). Of these names, 27 are currently recognized as valid subgenera (Bailey and Gosline 1955; Collette 1965; Cole 1967; Collette and Knapp 1967; Page 1974) of the three genera: *Ammocrypta* (*Ammocrypta* and *Crystallaria*); *Percina* (*Alvordius, Cottogaster, Ericosma, Hadropterus, Hypohomus, Imostoma, Odontopholis, Percina*, and *Swainia*); and *Etheostoma* (*Allohistium, Austroperca, Boleosoma, Catonotus, Doration, Etheostoma, Hololepis, Ioa, Microperca, Nothonotus, Litocara, Oligocephalus, Psychromaster, Ulocentra, Vaillantia*, and *Villora*).

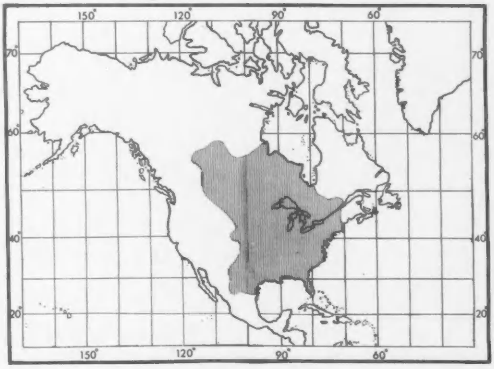

FIG. 5. Native distribution of the darters, tribe Etheostomatini.

Percina

The subgenera are listed in order from primitive to advanced following Page (1974).

Hadropterus Agassiz

Hadropterus Agassiz 1854: 305. Type-species *Hadropterus nigrofasciatus* Agassiz 1854, by monotypy.

Plesioperca Vaillant 1873: 36. Type-species *Plesioperca anceps* Vaillant 1873 (= *Hadropterus nigrofasciatus* Agassiz 1854), by monotopy.

Serraria Gilbert 1884: 205. Type-species *Hadropterus scierus* Swain 1883, by original designation.

Swainia Jordan and Evermann

Swainia Jordan and Evermann 1896: 1040. Type-species *Etheostoma squamatus* Gilbert and Swain 1887, by original designation.

Alvordius Girard

Alvordius Girard 1859a: 68. Type-species *Alvordius maculatus* Girard 1859a, by monotypy.

Ericosma Jordan

Ericosma Jordan 1877: 8. Type-species *Alvordius evides* Jordan and Copeland 1877, by original designation.

Odontopholis Page

Odontopholis Page 1974: 84. Type-species *Etheostoma cymatotaenia* Gilbert and Meek 1887, by original designation.

Hypohomus Cope

Cottogaster Cope 1869: 210. Type-species *Cottogaster aurantiacus* Cope 1869, by monotypy, preoccupied by *Cottogaster* Putnam 1863.

Hypohomus Cope 1870: 449. A replacement name for *Cottogaster* Cope 1869, preoccupied by *Cottogaster* Putnam 1863; same type-species as *Cottogaster* Cope, *Cottogaster aurantiacus* Cope 1869.

Cottogaster Putnam

Cottogaster Putnam 1863: 4. Type-species *Boleosoma tessellatum* Thompson 1853, not of DeKay (= *Rheocrypta copelandi* Jordan 1877), by monotypy.

Rheocrypta Jordan 1877: 9. Type-species *Rheocrypta copelandi* Jordan 1877, by monotypy.

Anemoces Jordan 1929: 156. Type-species *Ulocentra gilberti* Evermann and Thoburn *in* Jordan and Evermann 1896 (= *Rheocrypta copelandi* Jordan 1877), by original designation.

Imostoma Jordan

Imostoma Jordan 1877: 49. Type-species *Hadropterus shumardi* Girard 1859, by original designation.

Percina Haldeman

Percina Haldeman 1842: 330. Type-species *Perca nebulosa* Haldeman 1842 (= *Sciaena caprodes* Rafinesque 1818), by monotypy.

Pileoma DeKay 1842: 16. Type-species *Pileoma semifasciata* DeKay 1842 (= *Sciaena caprodes* Rafinesque 1818), by monotypy.

Asproperca Heckel *in* Canestrini 1860: 311. Type-species "*Asproperca zebra* Heck." (= *Sciaena caprodes* Rafinesque 1818), by monotypy.

Percina is the most primitive genus of Etheostomatini. The lateral line is complete from opercle to hypural plate and extends onto one or more scales on the caudal fin in several subgenera (Page 1977). The cephalic lateralis canals are complete. *Percina* differs from all other genera of Percidae in the presence of a row of enlarged and modified midventral scales on the bellies of males that probably function in stimulation of the female during spawning (Page 1976). Monophyly of *Percina* is supported by work with lactate dehydrogenase isozymes (Page and Whitt 1973b). Page (1974) has defined the subgenera of *Percina* through the use of a numerical taxonomy program. Etnier (1976) has revised the diagnosis of *Percina* (*Imostoma*) on the basis of his recognition of five species in the subgenus.

Ammocrypta

Two subgenera are recognized, *Ammocrypta* with six species and *Crystallaria* with one.

Ammocrypta

Pleurolepis Agassiz *in* Putnam 1863: 5. Type-species *Pleurolepis pellucidus* Agassiz *in* Putnam 1863 by monotypy; preoccupied by *Pleurolepis* Quenstadt 1852, Semionotidae.

Ammocrypta Jordan 1877: 5. Type-species *Ammocrypta beanii* Jordan 1877, by original designation.

Vigil Jordan 1919: 344. Substitute name for *Pleurolepis* Agassiz 1863, preoccupied by *Pleurolepis* Quenstedt 1852, Pisces; same type-species as *Pleurolepis* Agassiz, *Pleurolepis pellucidus* Agassiz *in* Putnam 1863.

Crystallaria

Crystallaria Jordan and Gilbert *in* Jordan 1885: 866. Type-species *Pleurolepis asprellus* Jordan 1878 by original designation.

Ammocrypta is intermediate phylogenetically between *Percina* and *Etheostoma*. *Ammocrypta* lacks the specialized midventral scales found in males of *Percina*. The lateralis system in *Ammocrypta* is similar to that in *Percina* but the number of preoperculomandibular pores is reduced from ten to eight or nine in some species. Williams (1975) diagnosed the subgenus *Ammocrypta* and revised the six species of the subgenus.

Etheostoma

The subgenera are listed in order from primitive to advanced following Bailey and Gosline (1955), Collette (1965), Page (1977), and L. M. Page (personal communication).

Ioa Jordan and Brayton

Ioa Jordan and Brayton 1878: 88. Type-species *Poecilichthys vitreus* Cope 1870, by original designation.

Allohistium Bailey

Allohistium Bailey *in* Bailey and Gosline 1955: 6. Type-species *Etheostoma cinerea* Storer 1845, by original designation.

Etheostoma Rafinesque

Etheostoma Rafinesque 1819: 419. Type-species *Etheostoma blennioides* Rafinesque 1819, by subsequent designation of Agassiz (1854: 305). Verified by Opinion 14, Int. Comm. Zool. Nomencl. 1910, Smith. Inst. Publ. 1938: 25–27. Not *Etheostoma flabellaris* Rafinesque 1819, as designated by Jordan and Gilbert 1877: 85.

Diplesion Rafinesque 1820: 37. Type-species *Etheostoma blennioides* Rafinesque 1819, by subsequent designation of Girard 1859b: 101 and Jordan and Gilbert 1877: 86.

Poecilosoma Agassiz 1850: 299. Type-species *Etheo-*

stoma variata Kirtland 1838, by subsequent designation of Agassiz 1854: 306. Name preoccupied by *Poecilosoma* Huebner 1819, Lepidoptera; *Poecilosoma* Stephens 1829, Hemiptera; and *Poecilosoma* Newman 1838, Coleoptera.

Poecilichthys Agassiz 1854: 304. A replacement name for *Poecilosoma* Agassiz 1850, preoccupied by *Poecilosoma* Huebner 1819, Lepidoptera; *Poecilosoma* Stephens 1829, Hemiptera; and *Poecilosoma* Newman 1838, Coleoptera; same type-species as *Poecilosoma* Agassiz 1850, *Etheostoma variatum* Kirtland 1838.

Hyostoma Agassiz 1854: 305. Type-species *Hyostoma newmanii* Agassiz 1854 (= *Etheostoma blennioides* Rafinesque 1819), by monotypy.

Nanostoma Putnam *in* Jordan 1877: 6. Type-species *Poecilichthys zonalis* Cope 1868, by original designation.

Rhothoeca Jordan 1885: 868. Substitute name for *Nanostoma* Putnam erroneously regarded as preoccupied by *Nannostomus* Günther; same type-species, *Poecilichthys zonalis* Cope 1869.

Ulocentra Jordan

Ulocentra Jordan 1878: 223. Type-species *Arlina atripinnis* Jordan 1877, by monotypy.

Boleosoma DeKay

Boleosoma DeKay 1842: 20. Type-species *Boleosoma tessellatum* DeKay 1842 (= *Etheostoma olmstedi* Storer 1842), by monotypy.

Arlina Girard 1859a: 64. Type-species *Arlina effulgens* Girard 1859a (= *Etheostoma olmstedi* Storer 1842), by monotypy.

Estrella Girard 1859a: 65. Type-species *Estrella atromaculata* Girard 1859a (= *Etheostoma olmstedi* Storer 1842), by monotypy.

Doration Jordan

Doration Jordan 1929: 156. Type-species *Boleosoma stigmaeum* Jordan 1877, by original designation.

Nothonotus Agassiz

Nothonotus Agassiz *in* Putnam 1863: 3. Type-species *Etheostoma maculatum* Kirtland 1840, by subsequent designation of Jordan and Gilbert 1877: 93.

Litocara Bailey

Litocara Bailey 1948: 79. Type-species *Poecilichthys sagitta* Jordan and Swain 1883, by original designation.

Austroperca Hubbs

Torrentaria Jordan and Evermann 1896: 1080. Type-species *Etheostoma australe* Jordan 1884, by original designation; preoccupied by *Torrentaria* (Hodgson MS) Gray 1863, Aves.

Austroperca Hubbs 1936: 1. A replacement name for *Torrentaria* Jordan and Evermann 1896, preoccupied by *Torrentaria* (Hodgson MS) Gray 1863, Aves; same type-species as *Torrentaria* Jordan and Evermann 1896, *Etheostoma australe* Jordan 1884.

Oligocephalus Girard

Oligocephalus Girard 1859a: 67. Type-species *Boleosoma lepida* Baird and Girard 1853, by subsequent designation of Vaillant (1873: 90).

Boleichthys Girard 1859b: 103. Type-species *Boleichthys exilis* Girard 1859b, by original designation.

Astatichthys Vaillant 1873: 106. Type-species *Etheostoma caeruleum* Storer 1845, by original designation.

Nivicola Jordan and Evermann 1896: 1082. Type-species *Poecilichthys borealis* Jordan 1884 (= *Boleichthys exilis* Girard 1859), by original designation; preoccupied by *Nivicola* Hodgson 1844, Aves.

Rafinesquiellus Jordan and Evermann 1896: 1082. Type-species *Aplesion pottsii* Girard 1859, by original designation.

Claricola Jordan and Everman 1896: 1093. Type-species *Etheostoma juliae* Meek 1891, by original designation.

Belophlox Fowler 1947: 1. Type-species *Belophlox mariae* Fowler 1947, by original designation.

Niviperca Whitley 1951: 68. A replacement name for *Nivicola* Jordan and Evermann 1896, preoccupied by *Nivicola* Hodgson 1844, Aves; same type-species as *Nivicola* Jordan and Evermann 1896, *Poecilichthys borealis* Jordan 1884 (= *Boleichthys exilis* Girard 1859).

Villora Hubbs and Cannon

Villora Hubbs and Cannon 1935: 11. Type-species *Villora edwini* Hubbs and Cannon 1935, by original designation.

Psychromaster Jordan and Evermann

Psychromaster Jordan and Evermann 1896: 1099. Type-species *Etheostoma tuscumbia* Gilbert and Swain 1887, by original designation.

Vaillantia Jordan

Vaillantia Jordan *in* Jordan and Brayton 1878: 89. Type-species *Boleosoma camurum* Forbes 1878 (= *Vaillantia chlorosomum* Hay 1880), by original designation.

Catonotus Agassiz

Catonotus Agassiz 1854: 305. Type-species *Catonotus lineolatus* Agassiz 1854 (= *Etheostoma flabellaris* Rafinesque 1819), by monotypy.

Richia Coker 1926: 106. Type-species *Richia brevispina* Coker 1926 (= *Etheostoma flabellaris* Rafinesque 1819), by original designation; preoccupied by *Richia* Grote 1887, Lepidoptera.

Richiella Coker 1927: 18. Substitute name for *Richia* Coker 1926, preoccupied by *Richia* Grote 1887, Lepidoptera; same type-species as *Richia* Coker 1926, *Richia brevispina* Coker 1926 (= *Etheostoma flabellaris* Rafinesque 1819).

Hololepis Agassiz

Hololepis Agassiz *in* Putnam 1863: 4. Type-species *Boleosoma barratti* Holbrook 1885 (= *Boleosoma fusiforme* Girard 1854), by subsequent designation of Jordan and Gilbert 1877: 93.

Copelandellus Jordan and Evermann 1896: 1100. Type-species *Poecilichthys quiescens* Jordan 1884 (= *Boleosoma fusiforme* Girard 1854), by original designation.

Microperca Putnam

Microperca Putnam 1863: 4. Type-species *Microperca punctulata* Putnam 1863 (= *Etheostoma microperca* Jordan and Gilbert *in* Jordan 1888), by monotypy.

Etheostoma is the most highly evolved and speciose genus of the Etheostomatini with 16 subgenera and about 101 species. Both the body lateral line and the cephalic lateralis system are variously reduced or interrupted in many of the subgenera of *Etheostoma* (Page 1977). Monophyly of *Etheostoma* is supported by work with lactate dehydrogenase isozymes (Page and Whitt 1973a). No thorough analysis has been published for all the subgenera of *Etheostoma* although several subgenera have been diagnosed recently (*Etheostoma* by Richards 1969; *Ulocentra* by Bouchard 1977; *Boleosoma* by Cole 1967; *Nothonotus* by Zorach 1972; *Villora* by Collette and Yerger 1962; *Psychromaster* by Bailey and Richards 1963; *Catonotus* by Kuehne and Small 1971; and *Hololepis* by Collette 1962) and work is in progress on other subgenera (L. M. Page personal communication).

LUCIOPERCINAE

Percidae with the anteriormost interhaemal not larger than posterior interhaemals; anal spines weak; lateral line extending onto caudal fin with supplementary lateral lines above and below it (one or both supplementary lateral lines sometimes absent in *Romanichthys*).

Luciopercini Jordan and Everman 1896

Luciopercinae reaching large size; nasal flap slightly developed on anterior nostril, absent on posterior; maxillary free posteriorly; well-developed canine teeth present except in *Stizostedion volgense*; swimbladder well developed; predorsal bone present, extending ventrally between first and second neural spines; supraoccipital crest well developed; body slightly compressed; breeding tubercles absent; vertebrae 42–50. One genus, *Stizostedion* Rafinesque, with five species, three in Europe and two in North America (Fig. 6). The European species are *S. lucioperca* (Linnaeus), *S. marinum* (Cuvier), and *S. volgense* (Gmelin); the American are *S. canadense* (Smith) and *S. vitreum vitreum* (Mitchill).

Stizostedion Rafinesque

Les sandres Cuvier 1817: 294. Based on *Perca lucioperca* Linnaeus.

Stizostedion Rafinesque 1820: 23. Type-species *Perca salmonea* Rafinesque (= *Perca vitrea* Mitchill) by monotypy.

Schilus Jarocki 1822: 224. Type-species *Perca lucioperca* Linnaeus by monotypy.

Lucioperca Schinz 1822: 475. Type-species *Perca lucioperca* Linnaeus by monotypy.

Lucioperca Fleming 1822: 394. Type-species *Lucioperca vulgaris* Fleming (= *Perca lucioperca* Linnaeus) by monotypy.

Sandat Cloquet 1827: 173. Type-species *Perca lucioperca* Linnaeus by original designation.

Lucioperca Cuvier *in* Cuvier and Valenciennes 1828: 110. Type-species *Perca lucioperca* Linnaeus by absolute tautonomy.

Sandrus Stark 1828: 465. Type-species *Perca lucioperca* Linnaeus by subsequent designation of Jordan 1917: 123.

Schilus Krynicki 1832, II: 441. Type-species *Schilus pallasi* Krynicki (= *Perca volgensis* Pallas) by subsequent designation of Jordan 1917: 176.

Cynoperca Gill and Jordan *in* Jordan 1877: 44. Type-species *Lucioperca canadensis* Smith by original designation.

Mimoperca Gill and Jordan *in* Jordan 1877: 44. Type-species *Perca volgensis* Pallas by original designation.

The five species of *Stizostedion* are large benthic predators. *Stizostedion lucioperca* is widespread in the Elbe River and eastward — basins of the Baltic, Black, Azov, Caspian, and Aral seas — and in the Maritsa River, which empties into the Aegean Sea. It is present throughout the Neva Basin, including lakes Ladoga, Il'men', and Onega. In Finland, it extends north to 64°N and, sporadically, to the Arctic Circle in the Baltic Sea basin. It is a large predator that inhabits slow-running rivers and large well-oxygenated lakes. It has been introduced in many French rivers (Goubier 1975). *Stizostedion volgense* is restricted to the main rivers in the basins of the Volga (Kama and Vyatka), Ural, Don, Dnieper, Bug, Dniester and Danube rivers. *Stizostedion marinum* lives in the brackish northwestern part

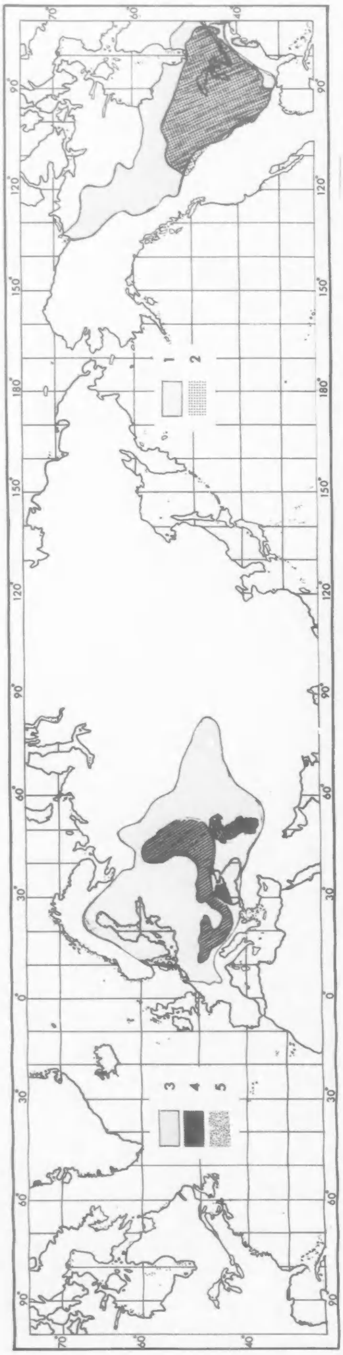

FIG. 6. Native distributions of the species of *Stizostedion*. (1) *S. vitreum*; (2) *S. canadense*; (3) *S. lucioperca*; (4) *S. volgense*; (5) *S. marinum.*

of the Black Sea and the Caspian Sea and rarely enters rivers. *Stizostedion canadense* is found from the Hudson Bay basin — including the Saskatchewan, Red, and Assiniboine rivers — the Great Lakes, and New Brunswick south to West Virginia, the Tennessee River in Alabama, eastern Oklahoma, the Red River in Texas, eastern Kansas, Nebraska, Wyoming, southwestern Iowa and Montana. The range of *S. vitreum vitreum* extends considerably farther north, even farther than that of *Perca flavescens*: from near the Arctic coast in the Mackenzie River southeastward through Quebec to the St. Lawrence River and southwards to the Gulf Coast in Alabama (Scott and Crossman 1973). There is also a residual stock, apparently native, along the Atlantic coast from Pennsylvania to North Carolina. It has been widely introduced outside of its native range, particularly in western U.S. reservoirs and along the Atlantic seaboard and elsewhere in North America. A subspecies, *S. vitreum glaucum* Hubbs, inhabited the deeper and clearer waters of Lake Erie, particularly in the eastern two-thirds of the lake. Regier et al. (1969) suggested that introgression with *S. v. vitreum* may have led to the disappearance of *S. v. glaucum* in Lake Erie.

The best recent sources of information on the systematics, morphology, and distribution of the European species of *Stizostedion* are Berg (1949), Berinkey (1958), Svetovidov and Dorofeeva (1963), and Shcherbukha (1967, 1974). There are two detailed osteological studies of species of *Stizostedion*: Pugliesi (1910) on *S. lucioperca* and Berinkey (1958) on *S. lucioperca* and *S. volgense.*

Romanichthyini Dumitrescu, Bănărescu, and Stoica 1957

Luciopercinae reaching small to moderate size; nasal flaps well developed on both anterior and posterior nostrils; maxillary concealed posteriorly; canine teeth absent; swimbladder absent; predorsal bone absent; supraoccipital crest moderately developed; body depressed or fusiform; breeding tubercles developed in both sexes; vertebrae 39–49. Two genera: *Zingel* Cloquet with 3 species: *Z. zingel* (Linnaeus), *Z. streber* Siebold, and *Z. asper* (Linnaeus); and the monotypic genus *Romanichthys valsanicola* Dumitrescu, Bănărescu, and Stoica.

Zingel Cloquet

Asperulus Schaeffer 1761: 58. Type-species *Zindel Ratisbonensium* Schaeffer (= *Perca zingel* Linnaeus) by subsequent designation of Jordan 1917: 16. Invalid as a work that is not consistently binomial (Opinion 345, Int. Comm. Zool. Nomencl.).

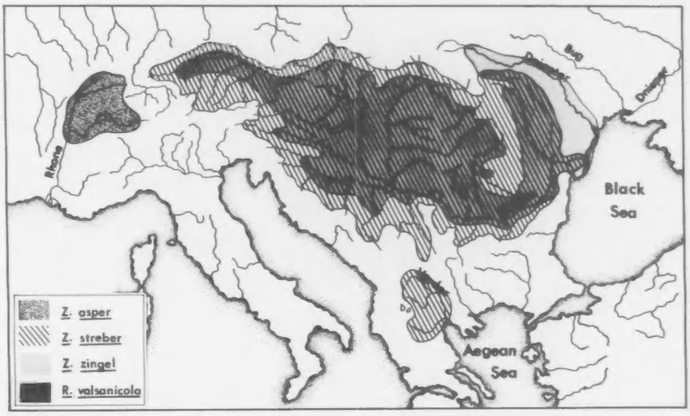

FIG. 7. Distributions of *Zingel* and *Romanichthys* (redrawn from Bănărescu 1964: fig. 295). (*Z. s. streber* in the Danube River; *Z. streber balcanicus* in the Vardar River.)

Asper Schaeffer 1761: 69. Type-species *Asper verus* Schaeffer (= *Perca zingel* Linnaeus) by subsequent designation of Jordan 1917: 16. Invalid as a work that is not consistently binomial (Opinion 345, Int. Comm. Zool. Nomencl.).

Asperulus Klein *in* Walbaum 1792: 584. Type-species *Perca zingel* Linnaeus by monotypy. By reprinting the names of Klein (1774), Walbaum did not give them nomenclatural status (Opinion 21, Int. Comm. Zool. Nomencl.).

Zingel Cloquet 1817: 240: Type-species *Perca zingel* Linnaeus by monotypy.

Zingel Jarocki 1822: 223. Type-species *Perca zingel* Linnaeus by absolute tautonomy.

Cingla Fleming 1822: 394. Type-species *Perca zingel* Linnaeus by monotypy.

Aspro Cuvier *in* Cuvier and Valenciennes 1828: 188. Type-spies *Perca asper* Linnaeus by subsequent designation of Jordan 1917: 124.

Zingel zingel is found in the Danube and its tributaries from Bavaria to the delta and in the Dniester (Fig. 7). It lives only in running water, usually in large deep rivers and never in flood plain lakes. *Zingel streber* is also found in the Danube and its tributaries from Bavaria to the delta as well as in the Vardar River, which drains into the Aegean Sea. It is more rheophilic than *Z. zingel* and ascends farther upstream in tributaries. It has a much more slender body than *Z. zingel*, an adaptation to the more rapid waters which it inhabits. Both species feed on small bottom invertebrates. *Zingel asper* inhabits the Rhone basin and presumably has habits and ecological requirements similar to those of *Z. streber*. Karaman (1962), Bănărescu (1964), and Gruptche and Dimovski (1973) recognized the Vardar River population of *Z. streber* as the subspecies *Z. s. balcanicus* S. Karaman. The population of *Z. streber* from the Nera River in southwestern Romania may represent a third, undescribed subspecies related to *Z. s. balcanicus*. Other recent sources of information on the systematics and morphology of *Zingel* include Oliva (1960), Gheracopol et al. (1970), and Smirnov (1971).

Romanichthys Dumitrescu, Bănărescu, and Stoica

Romanichthys Dumitrescu, Bănărescu, and Stoica 1957: 225–6. Type-species *Romanichthys valsanicola* Dumitrescu, Bănărescu, and Stoica by original designation.

Romanichthys valsanicola was confined to three tributaries (Arges, Vilsan, and Riul-Doamnei) of the upper Arges River (Fig. 7), a tributary to the Danube in Romania (Stănescu 1971).

It is now extinct in the Arges and Riul-Doamnei rivers because of construction of dams, deforestation, road construction, poisoning of the water, agrotechnical activity, and competition with species of Cyprinidae in the warmer waters caused by man's activity (Stănescu 1971). However, it has been collected in 1976 in the Vilsan River. It lives in piedmont rivers, frequently hiding under stones. Its food is mainly Plecoptera, but other rheophilic insects are also eaten.

Zoogeography

Perca (or presumably a *Perca* ancestor) probably differentiated in Europe from some anadromous offshoot of the Serranidae. Evidence from scale structure (McCully 1962) suggests that percids originated from anadromous serranids during the Cenozoic.

The Percidae may have dispersed over a North Atlantic land route at the end of the Cretaceous or beginning of the Eocene, when a connection between Europe and North America still existed. Arguments against their dispersal over a Pacific route are: absence of the family in East Asia, its scarcity in Siberia, absence of endemic species in Middle Asia and the Caucasus, and absence of the Romanichthyini east of the Dniester. Since there are more basic groups in Europe, it seems probable that the family first appeared in the fresh waters of Europe and soon dispersed to North America. After the Eocene interruption of the contact between the two continents, their percid faunas evolved independently: the Percini and Luciopercinae in Europe, the Etheostomatini in North America.

During the Oligocene, a contact was established between Europe and Siberia and some percid genera entered Siberia; later (in the Neogene), *Perca* and *Stizostedion* dispersed from Siberia to North America by a North Pacific route. The Siberian Neogene fauna of Percidae was probably richer than the present one, but always poorer than the European. During the Palaeogene the center of evolution of Old World Percidae was probably northern, especially northeastern, Europe. Up to the Oligocene or Miocene, the Percidae probably played a more important role in the fish fauna of Europe than now. In the Oligocene, the Cyprinidae entered Europe. Like many other Ostariophysi, the Cyprinidae are, wherever they occur, successful competitors. This is presumably due to the combination of such adaptations as increased hearing ability, possession of a warning substance (Schreckstoff), and protractile premaxillae (Collette et al. 1977). The early penetration of several stocks of Cyprinidae in Europe may have stopped the diversification of the Percidae. In North America the Cyprinidae entered during the Miocene and were represented by a single, rather primitive and less competitive stock; the three genera of American Etheostomatini were able, therefore, to undergo further differentiation. The only large piscivorous North American cyprinid is the genus *Ptychocheilus* and it is restricted to the western United States out of the native range of Percidae.

Both *Gymnocephalus* and *Percarina* are apparently derived from *Perca*. There are two subgenera of *Gymnocephalus* according to Holčík and Hensel (1974): the more primitive subgenus *Acerina* with *cernuus* and its offshoot *baloni* and the more advanced subgenus *Gymnocephalus* with *acerina* and *schraetser*. The ancestor of *Perca fluviatilis* probably was even more widespread in Europe and Asia than *P. fluviatilis* is today. The Asiatic highlands species *P. schrenki* and the North American species *P. flavescens* are derived from *P. fluviatilis*. In North America, the Etheostomatini arose from some unknown percid ancestor in response to unexploited ecological niches in fast streams. The most primitive genus, *Percina*, gave rise to *Ammocrypta* and *Etheostoma*, which further exploited the lotic niche in moderate to small streams. Isolation in many small stream systems has led to the evolution of numerous species of *Percina* and *Etheostoma*. The evolution of the Etheostomatini repeatedly shows miniaturization as an adaptation to restricted food supplies or spawning and nursery grounds in small streams. Correlated with reduction in size and rheophilic habits are the loss of a functional swimbladder and a reduction in the development of the lateral line on the body and head.

The tribe Romanichthyini developed from the Luciopercini in response to the same type of selective pressure that led, in North America, to the evolution of the Etheostomatini from the Percini. There has been a similar reduction in size and loss of the predorsal bone in the shift from life in larger slow-moving bodies of water to smaller stream habitats. The center of evolution of the Romanichthyini (and probably of European percids in general) was in the Danube River. The common ancestor of the Romanichthyini gave rise to *Zingel* and *Romanichthys*. *Zingel* twice colonized the Danube, giving rise to the two Danube species, *Z. streber* and *Z. zingel*. Later, an ancestor of *Z. streber* invaded the Rhone River through Doubs River (Steinmann 1938), leading to the evolution of *Z. asper*. It is also possible that the tribe once had a wider range and included more taxa (now extinct without offshoots), and the dispersal history may have been more complicated. *Romanichthys valsanicola*, endemic in a few Romanian tributaries of the Danube, is the smallest and most specialized member of the Luciopercini, and resembles most, through convergence, members of the Etheostomatini. As the most specialized lotic European percid, *Romanichthys* could not spread through Pliocene lakes and has remained isolated in the Arges River until present times.

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Perca fluviatilis in Australia: Zoogeographic Expression of a Life Cycle in Relation to an Environment[1]

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WEATHERLEY, A. H. 1977. *Perca fluviatilis* in Australia: zoogeographic expression of a life cycle in relation to an environment. J. Fish. Res. Board Can. 34: 1464–1466.

Perca fluviatilis was introduced into Australia during the nineteenth century. Its extensive distribution in Australia and the range of climatic and topographic conditions over which it occurs make it possible to distinguish the roles of high temperature, breeding conditions, and flow characteristics in rivers in limiting the spread of the species. By extrapolation the distributional limits of the species throughout the world can be largely explained and, by analogy, those of the closely related species *P. flavescens* in North America. A model of a fish life cycle arising out of knowledge of *Perca* life cycles is presented as a possible tool for clarifying and predicting the success or failure of species introduced into new environments.

Key words: Percidae, *Perca*, zoogeography, life history, introduction in Australia, predictive model, management, Eurasian perch

WEATHERLEY, A. H. 1977. *Perca fluviatilis* in Australia: zoogeographic expression of a life cycle in relation to an environment. J. Fish. Res. Board Can. 34: 1464–1466.

Perca fluviatilis fut introduite en Australie au dix-neuvième siècle. Sa répartition étendue en Australie et la gamme de conditions climatiques et topographiques dans lesquelles elle se trouve permettent de distinguer le rôle d'une température élevée, des conditions de la reproduction et du débit des rivières dans la limitation de la dispersion de l'espèce. On peut expliquer en grande partie, par extrapolation, les limites de l'aire de l'espèce dans le monde et, par analogie, celles de l'espèce étroitement apparentée, *P. flavescens*, en Amérique du Nord. L'auteur présente un modèle d'un cycle biologique de poisson dérivé des cycles biologiques de *Perca*. Le modèle peut servir à clarifier et à prédire le succès ou l'échec d'espèces introduites dans des environnements nouveaux.

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THE present paper summarizes the action of certain environmental factors (principally high temperature, topography, and spawning substrates), on several stages of the life cycle of *P. fluviatilis* in Australia and elsewhere, which determine the limits of its range (Weatherley 1963, 1974; Weatherley and Lake 1967). It also interprets the range of limits of *P. flavescens* in similar fashion (Weatherley 1963; see also Hokanson 1977; Thorpe 1977).

The range and distribution of a species is an outcome of factors which tend to disperse its members and factors that oppose their dispersal. Within its range the distribution of a species is determined by its ability to gain access to habitats that favor its survival. To obtain significant insight into the operation of these principles a view is required of the life cycle of the species and its responses to some of the more significant environmental factors.

Various Factors Affecting Range and Distribution of *Perca fluviatilis* and *P. flavescens*

I have recounted in earlier papers (Weatherley 1963, 1974; Weatherley and Lake 1967) the introduction of *P. fluviatilis* to Australia, beginning with Tasmania in 1861 and Victoria in 1868. The salient features of the *P. fluviatilis* distribution, as described elsewhere, were discerned initially in the Australian distribution. In Australia there are large distances and a wide array of climatic and topographic features, without the complication of excessive man-made alterations to aquatic conditions, or the presence of major political boundaries. This allowed one to consider the entire distribution on both microcosmic and macrocosmic scales, in the form of Tas-

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mania and of the Murray–Darling River system of continental Australia, respectively. The arguments concerning distribution thereby developed for *P. fluviatilis* were subsequently extended and tested against the world distribution of the species, and also for the distribution of the closely related species *P. flavescens* in North America.

The major factors limiting the ranges of *Perca* spp. can be epitomized as follows (Weatherley 1963, 1974; Weatherley and Lake 1967): (a) their dispersal from their foci of original introduction is a result of their swimming abilities (Weatherley 1963, 1974; Weatherley and Lake 1967; Hokanson 1977), which are by no means spectacular; (b) spawning substrate needs, typically fixed aquatic vegetation, though non-living materials may also be used; (c) thermal tolerance, 30–31°C being the ultimate upper lethal temperature; (d) salinity tolerance (about 50% seawater), which prevents entry of coastal waters and hence colonization of rivers through their estuaries.

Though I do not consider that factors other than the above are important in influencing the range of *P. fluviatilis* in Australia, other data on the species may be consulted as follows: Weatherley (1963, 1967, 1974), Lake (1967a), Williams (1967), and Weatherley and Lake (1967) give various data on the physical limnology of the Murray–Darling River system, and Weatherley (1963, 1974), Weatherley and Lake (1967) and Williams (1967) give limnological data on perch waters in Tasmania.

Foods eaten by *P. fluviatilis* in Australia, reported by Butcher (1945), Lake (1959, 1971), and Weatherley and Lake (1967), resemble those of the same species in European waters as reported by Allen (1935), Deelder (1951), Thorpe (1977), Popova and Sytina (1977), and Spanovskaya and Grygorash (1977).

Growth, spawning, development — Lake (1959) reported *P. fluviatilis* which weighed as much as 10 kg at capture (though a weight range of 0.1–1 kg is more usual), and growth to 35.3 cm in 22 mo in ponds in New South Wales (Lake 1971). The latter is a high rate (Thorpe 1977), probably attributable to the high mean water temperatures (Hokanson 1977; Weatherley and Lake 1967).

Perch begin to spawn in the Murray–Darling about 12°C (Lake 1959; Weatherley 1963), which is similar to that in Windermere (Le Cren 1951; Jenkin 1942). In eastern Australia perch may spawn in the highest temperatures (up to 15°C) known for the species (Weatherley 1963). However, Thorpe (1977) showed, in a plot of worldwide data of spawning temperatures in relation to latitude for both species of *Perca*, that *P. fluviatilis* fits precisely where expected — so the reproduction temperature is not anomalous. Lake (1967b) suggested a possible disruption of egg development by high prespawning temperatures in Australia, but this becomes unlikely on the realization that *P. flavescens* can produce viable spawn over the ambient range 3.9–18.6°C (Jones et al. 1976, cited by Hokanson 1977). Thorpe (1977) showed that relative fecundity data from Lake (1967c) are in the normal range for *P. fluviatilis* and *P. flavescens*, and hatching rates of *P. fluviatilis* (Lake 1967c) are similar to those of *P. flavescens* at the same temperature range (Hokanson 1977).

Fish of other species — While interactions with other species do occur, especially with indigenous eels, it is not likely that such species influence the distribution of *P. fluviatilis* in Australia to a major extent (Weatherley and Lake 1967; Lake 1971).

Predicting and Evaluating Success in Fish Introductions

It is obvious from the records of attempts to introduce fish species to new environments that there is no generally recognized formal procedure. The usual approach follows from an observation that a particular indigenous fish community lacks a sizeable "top predator" species suitable for sport angling, or that there are no very palatable species present, or some comparable criticism. Sometimes, during the search for a species to "improve" the fish community, some concern is given to such fundamental questions as whether the introduced species will be able to complete its life cycle in its new environment! That kind of question, if asked, makes us realize immediately that food, enemies, pathogens, the properties of the physicochemical environment, and suitable spawning substrates will determine, by their presence or absence, whether a species will be able to survive in a new environment.

Two kinds of biologists stand to gain from a better-planned approach to fish introductions: fishery managers, because they can try to predict rationally the chances of success in establishing a new species, and in cases of failure will have a better chance of understanding its causes; and ecologists, because every attempt at an introduction, successful or not, can be an illuminating large-scale experiment in which the otherwise hypothetical influences, discussed by zoogeographers, that determine ranges and distributions can be actually tested.

Figure 1 depicts a scheme for considering the life cycle of a species in relation to factors that facilitate or oppose progress from one life stage to the next. It can be used as a tool for predicting success of a new introduction of a species or helping to understand reasons for the failure of such an introduction. The more information available on the physicochemical and nutritional requirements, enemies, competitors, pathogens for each life stage of a species, the more useful such a scheme will be. And the greater the amount of information on the potential or actual

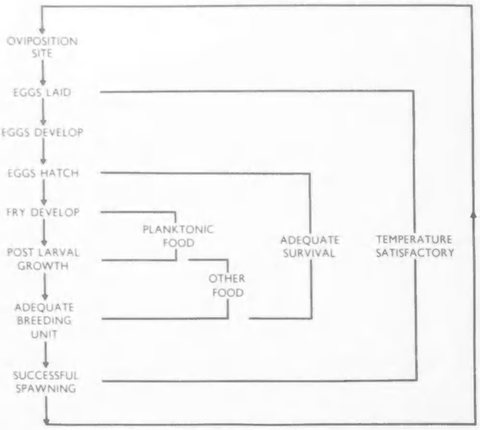

FIG. 1. Scheme of fish life cycle for use in predicting success or failure on introduction of a species to a new environment. The figure is a scaffolding, linking life stages, and implies the need for many quantitative details. Listed are the life stages which have different environmental requirements for temperature, nutrition, etc. These can be assigned real, estimated, or hypothetical values for survivorship based on knowledge of the population biology in relation to what is known of the new environment. Forms of mortality are various and will differ according to life stage, e.g., developing fry may die from density-induced food shortage, predation, pathogens, unsuitable temperatures, etc. Survivorship in the period of postlarval growth will be closely related to growth rate and hence food supply and temperature. The scheme invites those intending to introduce a species new to an environment to assign values to mortality rates between life stages that reflect as closely as possible the expected effects of living in the new environment given the known parameters of the population dynamics of the species, and the characteristics of the new environment. The life cycle stages that are particularly susceptible to the effects of food and temperature, and for which adequate survival is likely to be particularly threatened by environmental factors, are indicated.

environment for each stage the clearer it will become why a species will probably succeed or has succeeded in a new environment, or at which life stage(s) failure has occurred, and why. The scheme can also be useful in pinpointing the major points in life cycles where our knowledge fails to match our needs.

It would be possible to adapt the scheme to the investigation of effects of competitors, predators, angling pressures, etc., because it can, by inclusion of suitable numerical data, be converted into a visualizable life table.

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Retinal Structure and Function in the Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*)[1]

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ALI, M. A., AND M. ANCTIL. 1977. Retinal structure and function in the walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*). J. Fish. Res. Board Can. 34: 1467–1474.

In the sauger, *Stizostedion canadense*, the tapetum lucidum of the retina was found to be more highly developed than in the walleye, *S. vitreum vitreum*. The tapetum is uniformly distributed throughout the sauger's eye, whereas it reaches a comparable development only in the ventral region of the walleye's retina. Other structural differences also suggested that the sauger's retina is more sensitive to light than the walleye's. In both species, photomechanical changes in response to light- and dark-adaptation were restricted to the retinal epithelial pigment (melanin) and the rods. Electroretinographic recordings appeared to be correlated with the differences in tapetal development and habits of the two species.

Key words: Percidae, *Stizostedion vitreum vitreum*, *S. canadense*, light intensity, retinal structure, histology, electrophysiology, behavior

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Le doré jaune, *Stizostedion vitreum vitreum*, et le doré noir, *S. canadense*, manifestent un phototactisme négatif marqué au stade adulte et leur rétine possède un tapis réflecteur. Une étude détaillée de la structure rétinienne révèle que le tapis réflecteur de la rétine du doré noir contient plus de matière réflectrice, laquelle est plus ou moins uniformément répartie dans l'œil, alors que ce tapis n'atteint un développement comparable que dans la zone ventrale de la rétine du doré jaune. On signale quelques autres particularités qui suggèrent que la rétine du doré noir est plus sensible à la lumière que celle du doré jaune. Seuls les bâtonnets et le pigment épithélial sont impliqués dans les réponses rétinomotrices à la lumière ou l'obscurité chez ces deux espèces. Quelques enregistrements électrorétinographiques suggèrent également que le doré noir, qui préfère les cours d'eau passablement troubles, possède un appareil visuel mieux adapté à un environnement photique déficient.

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THIS is a report on a detailed comparative histological study of the walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) retinas, along with a comparison of the retinal sensitivities of the two species by measuring their flicker fusion frequencies (FFF) electroretinographically. ERG–FFF is the frequency at which the eye is incapable of distinguishing one flash from the following one, as indicated by a fusion of its electroretinogram (ERG). The ultrastructure of cones and the tapetum as well as the role of the cone ellipsoids as light guides have been described in an earlier study (Zyznar and Ali 1975).

In a preliminary study (Ali and Anctil 1968) we showed that the retinas of the walleye and sauger resemble each other in general structure, but that the walleye has a denser retinal epithelial pigment and less reflecting material. These differences were related to differences in habitat and behavior of these species, which are sympatric and negatively phototactic. The walleye grows well in clear and turbid waters, is primarily crepuscular and feeds at dawn and dusk whereas the sauger prefers extremely turbid waters and may feed intermittently throughout the day (R. A. Ryder unpublished data).

Materials and Methods

The specimens were collected mainly from Lac Prissac near Abitibi in the Province of Quebec. The total lengths of the fishes studied were about 10.5 cm for the walleye and about 14.0 cm for the sauger. The fish were held alive in the Montréal Municipal

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Aquarium (about 20°C) before being sampled or used in electrophysiological experiments. The daily light regime consisted of 16 h of light and 8 h of darkness. The energy value of the ambient light was 1.34 ± 0.30 μW/cm^2. All work whose results are presented here was carried out between May 1970 and June 1971.

Histological — Specimens were sampled during both day and night and were exposed to ambient room light or complete darkness for at least 3 h. They were beheaded and the eyes removed. The dorsal, dorso-temporal, temporal, ventro-temporal, ventral, naso-ventral, nasal, and naso-dorsal regions of the eyes were fixed in separate vials in Bouin's for 48 h. The material was then dehydrated and cleared in Dioxan and embedded in paraffin (mp 61°C). Tangential and transverse sections (6μm) were cut and stained with Harris' hematoxylin. Before counterstaining with eosin the sections were treated with acid alcohol to bleach the hematoxylin from nonnuclear regions, and then immersed in saturated lithium carbonate to emphasize the nucleoli. The stained sections were mounted in Permount.

Electrophysiological — Fish held at 20°C were used. Dark- or light-adapted fish were anesthetized (MS-222; 0.001%), rolled in gauze and held immobile in a plexiglas tray. Their electroretinograms (ERG), which indicate the difference in potential between the front and the back of the eye, were recorded with Ag–AgCl electrodes using a technique described earlier (Ali and Kobayashi 1967; Kobayashi and Ali 1971). When a flickering stimulus is created by rotating a sectored disc in front of the light source, each flash or flicker elicits one response. When the frequency of the flickering light is increased, the individual components of the ERG fuse with one another and, with a further increase in the stimulus frequency each ERG fuses with the following one so that it is impossible to relate the stimulus to the response (Hanyu and Ali 1964). The frequency at which this occurs is called the flicker fusion frequency (FFF). In the light-adapted state, a fish with a greater acuity of vision has a higher FFF value at any given intensity, in the dark-adapted state a more light sensitive fish attains maximum FFF values at lower light intensities. Thus, the ERG–FFF values shed considerable light on the structure and performance of the retina.

Histology

In both species the ventral region of the retina is more densely pigmented than the dorsal and temporal regions (Fig. 1). The pigment is distributed mainly in the epithelial cell bodies and at the vitread tips of these cell processes, though pigment granules are always found diffusely in the reflecting material itself. The tapetum is distributed in all the retinal regions; however, in the walleye retina it is better developed in the ventral region than in any other. Wunder (1930) reported the presence of tapetal material primarily in the dorsal two-thirds of the retina in the European percids *Gymnocephalus cernua* and *Stizostedion lucioperca* and Moore (1944) found it to have a wider distribution in the walleye.

Examination of light- and dark-adapted retinas (Fig. 1) indicates that among the visual cells only the rods undergo photomechanical changes, contrary to Moore's (1944) opinion, based on light-adapted material only, that the cone myoids of the walleye should display retinomotor movements. Observation of retinas light-adapted by night and dark-adapted by daytime reveals no endogenous retinomotor rhythm. In light-adapted retinas, the rod myoids are expanded and the rod outer segments are close to the epithelial cell bodies (Fig. 1C, D), whereas pigment aggregates at the tip of the tapetal processes. In dark-adapted retinas, the rod myoids are contracted and the rod outer segments form clusters hanging over the cone outer segments, whereas the remaining pigment has aggregated at the margin between the pigment cell processes and the rod clusters (Fig. 1A, B). This arrangement occludes the access of light to the rods and tapetum in the light-adapted state, but the cones remain exposed in scotopic conditions. The double cone myoids of the walleye are very short or almost nonexistent, and the single cone myoids are relatively elongate and always in an expanded position.

The cones of the walleye retina are larger and less numerous in the dorsal quarter than in the temporal region (Fig. 3, Table 1). The latter is the region of maximum cone density, i.e. the area retinae. The ventral region (of maximum tapetal development) resembles the dorsal and other regions and has very few single cones. The number of rods, which are very slender, is higher in the dorsal region than in the area retinae (Table 1). The rate of summation, e.g. the number of photoreceptor cells in relation to bipolar and ganglion cells, is greater in the dorsal and ventral regions and lowest in the temporal region (Table 1), at least at the photoreceptor/bipolar cell

FIG. 1. Transverse sections of the walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) retinas: dark-adapted ventral retina of the walleye (A) and the sauger (B); and light-adapted dorsal retina of the walleye (C) and the sauger (D). (ch, cone horizontal cell; D, double cone; G, tapetal processes infiltrated with melanin pigment; P, retinal epithelial pigment (melanin); R, rods; S, single cone.)

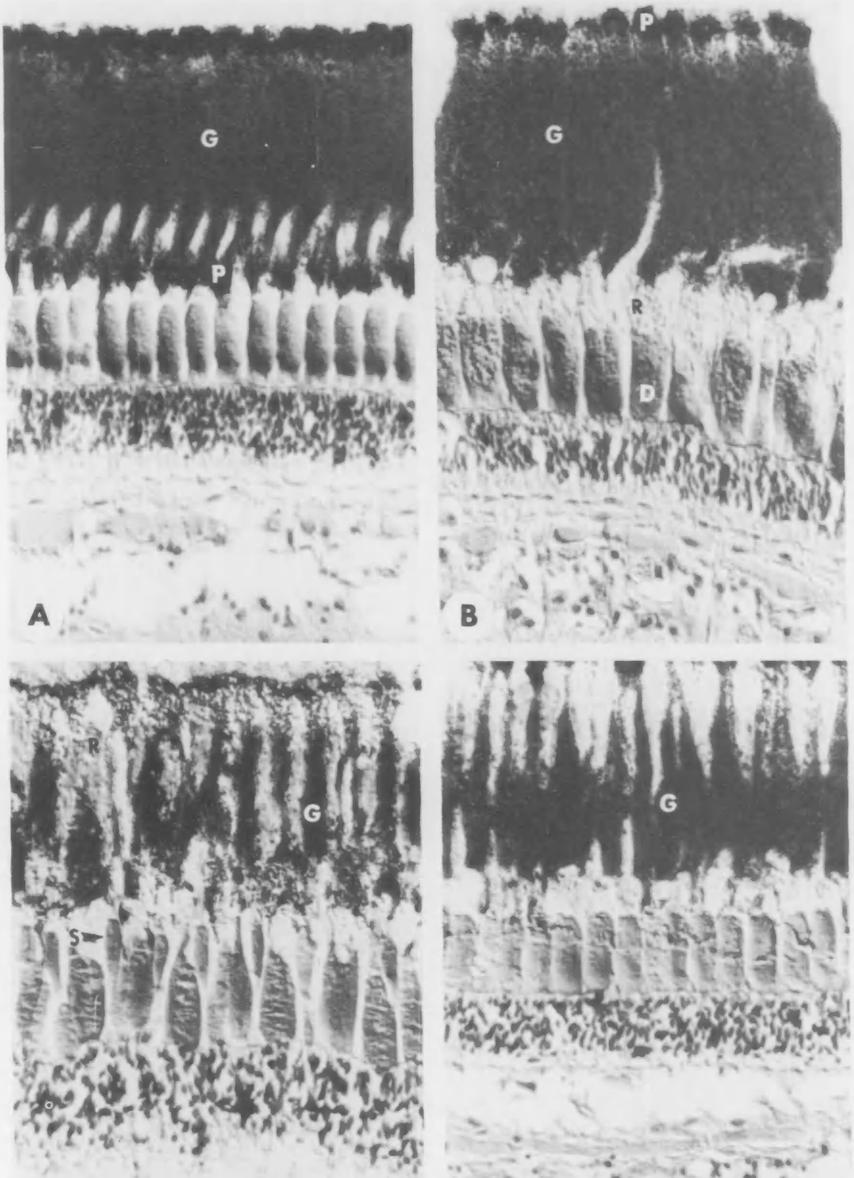

G
P
A
P
G
R
D
B
R
G
S
ch
C
G
D
50μ

TABLE 1. Numbers of visual cells in a 0.019 mm² area and rates of summation (photoreceptor: bipolar: ganglion cells) in the retinas of the walleye and sauger[a].

Region	Cones			
	Single	Double	Rod nuclei[b]	Rate of summation
		Walleye		
Dorsal	14	45	6274	132:6:1
Temporal	46	92	5018	136:8:1
Ventral	7	66	6092	172:6:1
		Sauger		
Dorsal	11	72	4017	182:4:1
Temporo-dorsal	41	128	4245	152:6.5:1
Temporal	43	116	3671	126:4:1
Temporo-ventral	29	96	3864	124:5:1
Ventral	57	148	3414	125:5:1

[a] Values taken from one retina of each species.

[b] Estimated according to cell count method described by O'Connell (1963).

integrative level. Also the walleye retina possesses huge horizontal cells (Fig. 2C, D), as noted by Moore (1944). Large horizontal cells are seen also in a microphotograph of the retina of *S. lucioperca* (Engström 1963). Selvin de Testa (1966) noted that horizontal cells of this size are often found in marine teleosts living in turbid waters. Figure 2C also shows a rod horizontal and a huge internal cone horizontal cell, according to Parthe's (1972) classification, and Fig. 2D shows two cone horizontal cells anastomosing with each other.

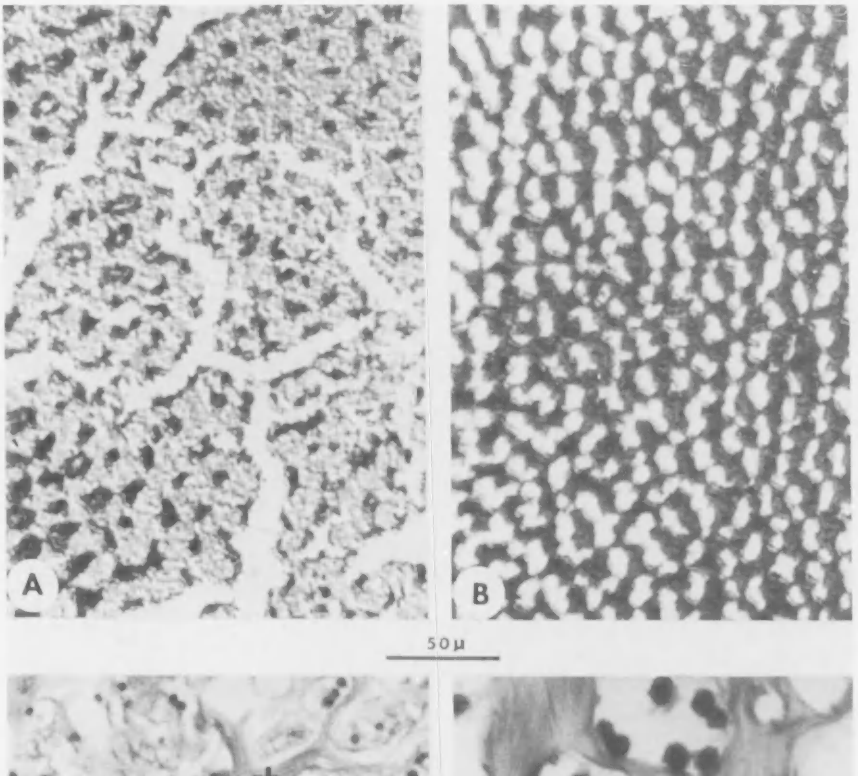
An inverse relationship was established between single cone density and tapetal development in the walleye and sauger retinas. This relationship is even more clear-cut in the retina of five families of fish (Argentinidae, Chlorophthalmidae, Zeidae, Serranidae, Scorpaenidae) equipped with a non-occlusible chorioidal tapetum (Tamura 1957) and in the two anchovies mentioned above (O'Connell 1963), all of which lack single cones. Similarly, the loose cone arrangements observed tangentially may be correlated with the "aberrant ecology" (Engström 1963) of the species possessing them, i.e. crepuscular or nocturnal habits, occurrence in dimly lit, turbid environments.

The tangential sections passing through the cone ellipsoids of the walleye's retina (Fig. 3) show that the temporal region has the C-type mosaic of Anctil's (1969) classification, i.e. flattened quadrangular arrangements of double cones with central single cones, or the G-type, i.e. square patterns of double cones all parallel to each other with single cones intercalated. All the other regions have patterns intermediate between the E-type (parallel rows of single and double cones) and the G-type. Moore (1944) figured a cone mosaic of the walleye similar to the E-type, and Engström (1963) described similar cone patterns in the retina of *S. lucioperca*.

A comparison of the sections confirms the previous observation (Ali and Anctil 1968) that the tapetal processes of the sauger's retina are more highly developed than those of the walleye. The granular tapetum of the sauger is about equally distributed in all the retinal regions, whereas the pigment granules are more abundant ventrally (Fig. 1B, D). In tangential or oblique sections of the light-adapted dorsal retina, the pigmented tapetal processes form a well developed reticular pattern overlying rod clusters (Fig. 2B), whereas the processes are thinner and sparse in the walleye's dorsal retina (Fig. 2A).

The tangential sections of the retina (Fig. 3) show that the diameter and density of the double cones vary more from region to region in the sauger than in the walleye. The area retinae is ventral in the sauger (Table 1, Fig. 3), although the dorso-temporal and temporal regions also have comparable cone densities. The sauger's cone mosaics are of the G-type, except in the temporo-nasal arc where they are of the E-type. The ratio

FIG. 2. Tangential sections of the retinas: section passing through the rods and tapetal processes in the dorsal retina of the walleye (A) and the sauger (B); section passing through the huge horizontal cells in the dorsal retina of the walleye (C) and the sauger (D). (ch, cone horizontal cell; rh, rod horizontal cell.)


A
B
50μ
rh
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C
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ch
D
25μ

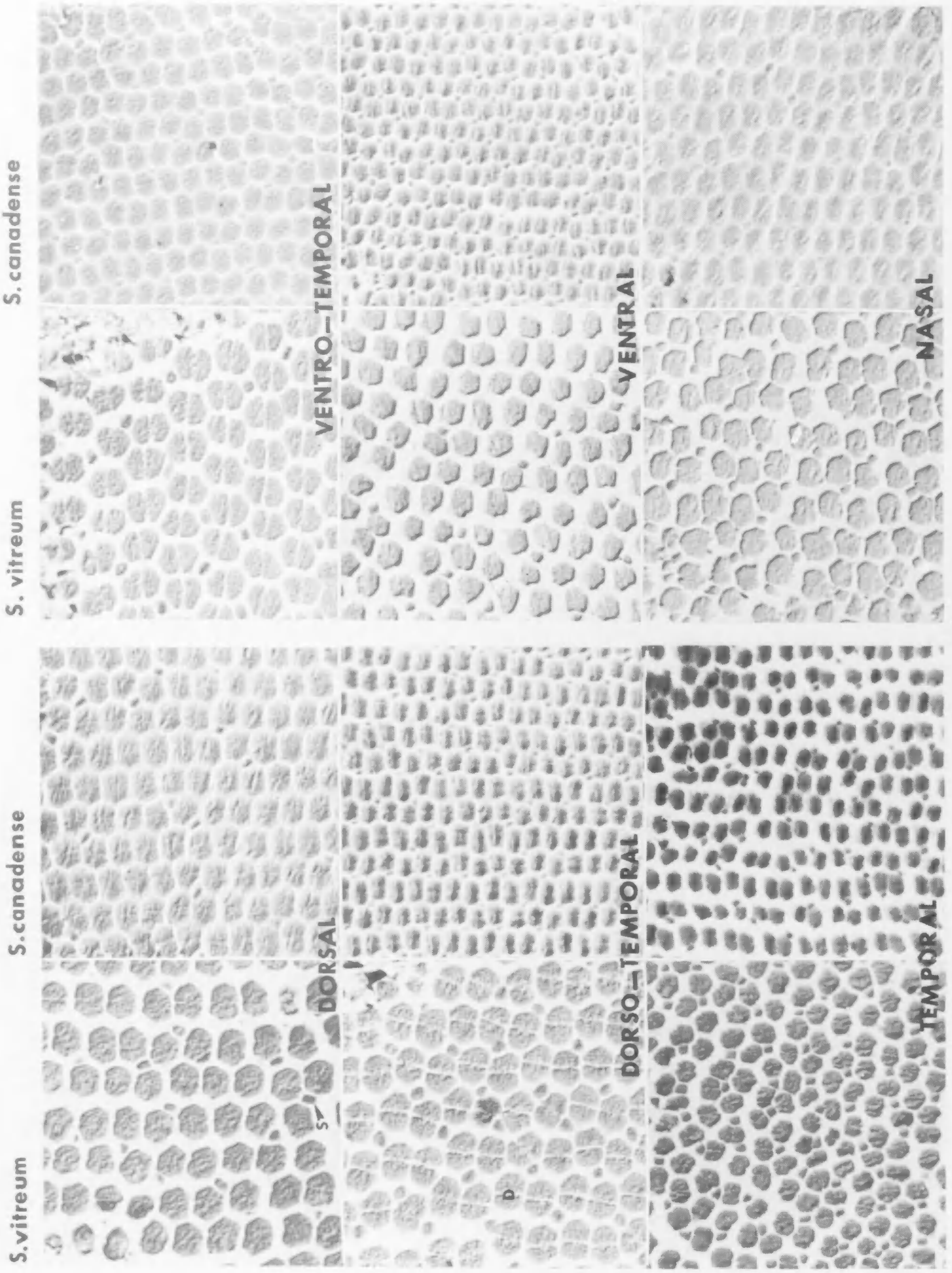
S.vitreum
S.canadense
S. vitreum
S. canadense
DORSAL
VENTRO—TEMPORAL
DORSO—TEMPORAL
VENTRAL
TEMPORAL
NASAL
S
D
100μ

FIG. 3. Tangential sections passing through the cone ellipsoids in various regions of the walleye and sauger retinas. (D, double cone; S, single cone.)

of single to double cones is lower than the area retinae of the walleye, and the rate of summation at the photoreceptor/bipolar cell level is greater in the retina of the sauger (Table 1) whereas the rods are not strikingly less abundant in the latter species.

Flicker Fusion Frequencies

In the light-adapted state there was practically no difference between the ERG–FFF's of the two species (Fig. 4). On the other hand, in the dark-adapted condition (Fig. 4) the maximum ERG–FFF values are attained at a lower light intensity in the case of the sauger than in the case of the walleye. Since these results are from only two (dark) and three (light) experiments, further detailed electroretinographic work with the two species appears desirable.

Discussion

These results suggest that the sauger's retina is better adapted than the walleye's for life in a dimmer environment. The features in support of this are (1) more reflecting material and a better organization of the epithelial cell processes of the retina, (2) the uniform distribution of the tapetum all over the retina, (3) a decrease in the relative abundance of single cones in the areae retinae and other regions, (4) an increase in the rate of summation at the photoreceptor/bipolar cell integrative level, and (5) the lower intensity thresholds required for maximum flicker fusion frequencies. The superior development of the tapetum in the sauger would permit more efficient reflections throughout the entire retinal surface and the consequent increase in sensitivity which has been observed in field studies (R. A. Ryder unpublished data). The other features mentioned above appear to be adaptations to increase sensitivity or adaptive adjustments as a result of the development of the tapetum lucidum.

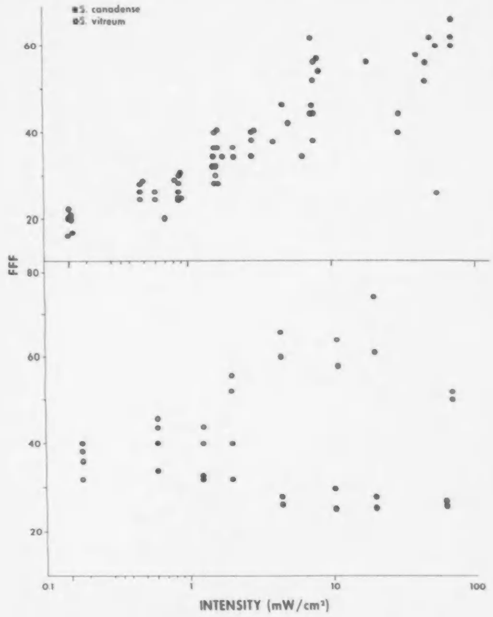

FIG. 4. Electroretinogram–flicker fusion frequency (ERG–FFF) of walleye (*S. vitreum vitreum*) and sauger (*S. canadense*) adapted to light (above) and to dark (below).

In both species photomechanical changes take place as an adaptation to differences in light intensity, but cones do not participate in this phenomenon. The cones of the seatrout (*Cynoscion*), which shares the presence of a structurally similar tapetum with *Stizostedion* spp., undergo restricted movements in the dark-adapted state (Arnott et al. 1972), but the end-result is the same in both: the cones are immersed among many small, contracted rods. These cone positions, like the permanently expanded myoids of the walleye and sauger single cones, are puzzling, yet they seem to reflect a transitional stage in the adaptive evolution of their retinomotor responses. At one extreme of this evolution, we have the cones of two anchovies equipped with an occlusible retinal tapetum which undergo extensive movements during dark-adaptation and are thus concealed apart from both rods and light access by the retinal pigment (O'Connell 1963).

Measurements of reflectivity and orientation of the reflecting material are not yet available for teleost eyes possessing a retinal tapetum lucidum. Denton and Nicol (1964) and Nicol (1969) have well demonstrated that the guanine crystal orientation of the chorioidal tapetum of sharks and sturgeons prevents the light scattering throughout the various retinal regions, thereby preventing a loss of sharpness of the visual image. It is not clear yet how the packed tapetal spheres (Arnott et al. 1972) or the tiny crystals stored in the retinal tapetal processes may achieve this in the teleosts. As the optics of this reflecting system in teleost eyes with retinal tapeta remain unknown, it is impossible to infer differences in reflecting efficiency from the structural differences in tapetal development observed in the walleye and sauger. Such studies may help to explain why only the ventral region of the walleye retina has attained a tapetal development similar to that of the sauger.

The ERG–FFF data for the dark-adapted fish (Fig. 4) show the possible influence of the greater development of the tapetum in the sauger's retina. At intensities about a log unit lower than for the walleye, the values for the sauger reach a saturation point. Although low intensities could not be used for technical reasons, it is reasonable to assume that the sauger's eye is sensitive to lower intensities of light. In this respect these results are similar to those obtained with the albino and pigmented brook trout, *Salvelinus fontinalis* (Ali and Kobayashi 1968). That investigation indicated that the albino, which lacks melanin pigment and therefore has greater reflexion within its eye, is more sensitive to lower light intensities and reaches a saturation ERG–FFF value also at a lower intensity.

The reason that there is practically no difference between the walleye and sauger in the light-adapted ERG–FFF values is easy to explain. In the light-adapted state, the tapetum is shielded by the melanin pigment expanded into the tips of the epithelial cell processes. This renders the two retinas similar by eliminating the differences in sensitivity brought about the greater reflexion caused by the greater tapetal development in the sauger's retina.

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Photoreceptors and Visual Pigments as Related to Behavioral Responses and Preferred Habitats of Perches (*Perca* spp.) and Pikeperches (*Stizostedion* spp.)[1]

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A review of the literature indicated contrasts in retinal structure and function between perches (*Perca* spp.) and pikeperches (*Stizostedion* spp.). Foremost among these were differences in size and distribution of rods, size and shape of cones, extent of retinomotor responses, possession or lack of reflecting material, and relative concentrations of melanin. The perches are primarily active by daylight, whereas the pikeperches are most active during twilight or at night. The coincidental occupancy of shoal areas by yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*) at twilight is related to decreasing visual acuity of the former and the approach of optimum visual performance in the latter species. On this basis the two species have a classic predator–prey relationship.

Key words: histology, light, *Perca* sp., photopic vision, predation, retina, *Stizostedion vitreum vitreum*, symbiosis, tapetum lucidum

ALI, M. A., R. A. RYDER, AND M. ANCTIL. 1977. Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perches (*Perca* spp.) and pikeperches (*Stizostedion* spp.). J. Fish. Res. Board Can. 34: 1475–1480.

On a noté des divergences de structure et de fonction dans la rétine entre les perchaudes (*Perca* spp.) et les dorés (*Stizostedion* spp.). Parmi celles-ci on a signalé des différences dans la taille et la répartition des bâtonnets, la taille et la morphologie des cônes, l'étendue des réponses rétinomotrices, la présence ou l'absence d'un tapis réflecteur et les concentrations de mélanine dans l'épithélium pigmentaire. Les perchaudes sont actives surtout durant le jour, tandis que les dorés accusent une activité maximale au crépuscule ou durant la nuit. L'occupation simultanée des hauts-fonds par la perchaude (*Perca flavescens*) et le doré jaune (*Stizostedion vitreum vitreum*) au crépuscule paraît reliée à la baisse de l'acuité visuelle chez la première espèce, et à la montée de la performance visuelle chez la deuxième espèce. C'est sur cette base que s'est établi une relation classique prédateur–proie entre ces deux espèces.

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DIFFERENCES in retinal structure and function among percids afford good examples of adaptations to diverse ecological conditions. This was first recognized by Wunder (1930) in his detailed study of a number of fishes, including percids, from Lake Balaton in Hungary. He noticed variations in the retinal epithelial pigment and tapetum lucidum and related these to the habitat and behavior of these fishes. Moore (1944) extended these studies to the retinas of the North American walleye (*Stizostedion vitreum vitreum*) and mooneye (*Hiodon tergisus*) and related the occurrence of a tapetum to the relatively turbid waters in which these fishes dwell. Recently, Burkhardt (1977) has found that the receptive

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fields of *Stizostedion* spp. cones have an antagonistic center — surround organization.

Differences in cone densities, distribution, and mosaics among the retinas of the Eurasian perch (*Perca fluviatilis*), pikeperch (*S. lucioperca*) and ruffe (*Gymnocephalus cernua*) have been related to differences in feeding habits of these fishes (Ahlbert 1969, 1975).

A preliminary investigation (Ali and Anctil 1968) showed differences in the development of the retinal epithelial pigment (REP) between the walleye and sauger (*S. canadense*) which could be related to habitat and habits. A subsequent study (Ali and Anctil 1977) confirmed this and provided additional support from electroretinographic (ERG) results. Both in the field and in the laboratory, differences between the yellow perch (*P. flavescens*) and two of the North American pikeperches (*Stizostedion* spp.) have been observed with regard to their distribution, growth, feeding, interactions, hardiness, and behavior. These and previous observations prompted a comparison of their photoreceptors and visual pigments with their behavior and preferred habitats. In this paper we have attempted to do this using available information, published and unpublished.

Photoreceptor Organization and Retinomotor Responses

There are significant differences in photoreceptor structure and organization between the perches (*Perca* spp.) and pikeperches (*Stizostedion* spp). Some of these features have been noticed in studies of living, isolated retinal cells (Anctil et al. 1973) and more recently from scanning electron micrographs particularly (Ali and Wagner 1977). The rods of the yellow perch are relatively large and evenly distributed, while the cones are of moderate size with smooth ellipsoids (Fig. 1, 2). In contrast, the rods of the pikeperches are extremely small and distributed in groups between the processes of the pigment epithelium (Fig. 3). The cones of the pikeperch retina are bulky (Fig. 3) and possess a granular ellipsoid. This granular appearance derives from hypertrophic mitochondria transformed into oil droplets. Moreover, only rods and the epithelial pigment are involved in the retinomotor responses of pikeperches (Ali and Anctil 1977), whereas cones participate also in the case of the yellow perch (Ali and Wagner 1977). Finally, the pigment epithelium of the pikeperch retina is densely packed with a reflecting material (Fig. 3), the tapetum lucidum, made of rectangular or square granules identified as 7,8-dihydroxanthopterin (Zyznar and Ali 1975). These granules, which have a high refractive index, are lacking in the yellow perch retina. On the other hand, there is very little melanin pigment in the pigment epithelium of the pikeperches, as opposed to the large concentrations found in the yellow perch (Ali and Anctil 1976).

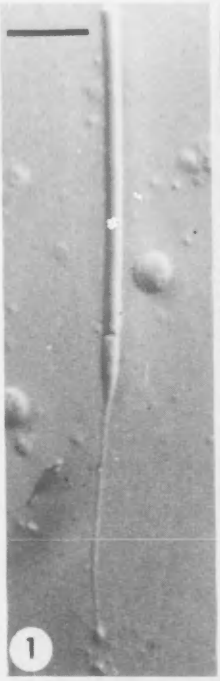
All these differences and specializations underscore the different modes of life of these percids. The pikeperches prefer turbid waters or crepuscular or nocturnal feeding activity; when in relatively clear waters they feed at dusk or night, while in turbid waters they may be intermittently active throughout the day (Ryder 1977). Hence, they display several retinal adaptations for functioning efficiently in low ambient light:

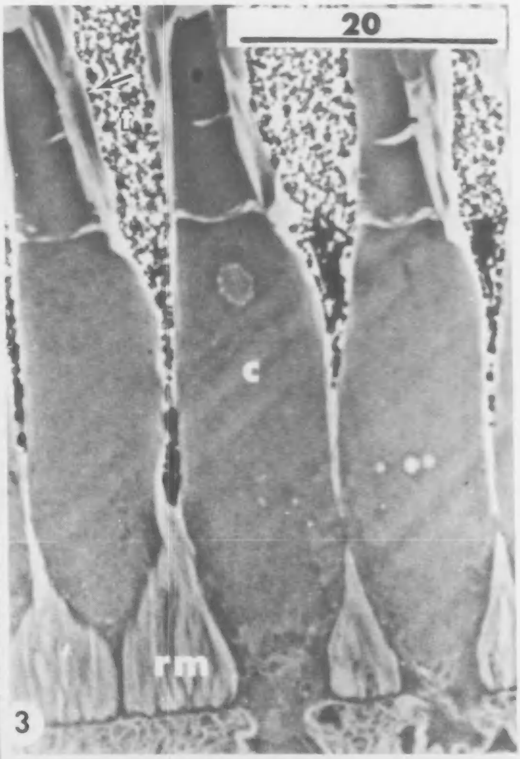
1. They possess a tapetum lucidum which acts as a diffuse reflector and increases the exploitation of the available dim light (Zyznar and Ali 1975).

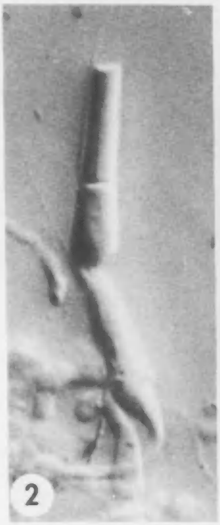
2. Cones being immobile, their position in the dark-adapted retina is in the direct path of the light impinging on the groups of rods, and the cone ellipsoid appears to collimate light by virtue of the droplets of mitochondrial origin. The result is a light-guide effect (Fig. 4), which increases retinal sensitivity greatly.

3. The position of the shielding melanin pigment in the light-adapted retina delimits the angle of acceptance of the cones and thus allows the concentration of light on each cone outer segment. In the dark-adapted state, the melanin pigment is interposed between the rod clusters and the tapetum, thus increasing the scattering effect of the tapetum on light passing through the cones. This also results in increased scotopic sensitivity. It is noteworthy that a similar result is obtained in the mooneye and the goldeye (*Hiodon* spp.), fishes that inhabit similar environments, by the grouping of cones in bundles (Wagner and Ali unpublished data); that is, the aggregated cones guide the light towards the groups of rods. This is a good example of convergence in physiological adaptation using divergent morphological means.

The yellow perch, on the other hand, thrives best in relatively clear, shallow water, is diurnal in behavior, and assembles readily in schools during daylight. Hence, its retina (Ali and Anctil 1976) is specialized for photopic conditions and lacks the tapetum lucidum, bulky cones, and other devices which enhance scotopic sensitivity. Structures such as cone droplets or slender rods, grouped and placed in the path of light funnels, are all absent in the yellow perch. Cones migrate away from the light path in the dark-adapted retina, as is usual in duplex retinas of arhythmic fishes. The large rods of the yellow perch are also less numerous than in the pikeperches and probably are less efficient for either nocturnal activity or adaptation to turbid waters.







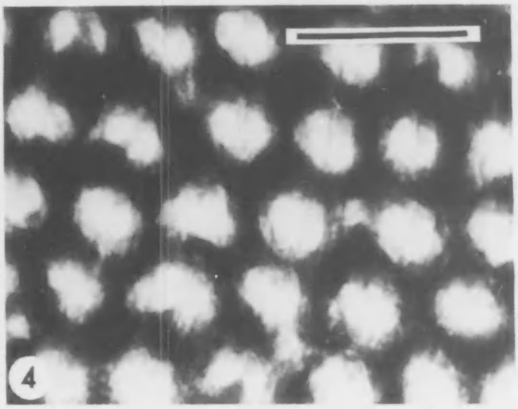


FIG. 1 and 2. Rod (1) and single cone (2) isolated from a yellow perch (*Perca flavescens*) retina by techniques described in Anctil et al. (1973). Scale for both figures is shown in Fig. 1 and represents 10 μm. FIG. 3. Transverse section through the dark-adapted retina of the sauger (*Stizostedion canadense*) viewed by phase contrast. Rod clusters are indicated by arrow. C, cone; rm, rod myoid; t, tapetum lucidum. Scale: 20 μm. FIG. 4. Bright-field optical micrograph of a fresh dark-adapted walleye (*S. vitreum vitreum*) retina focused at the level of the cone outer segments. Cone outer segments appear much brighter than surrounding rods, an indication of their light guide effect. Scale 30 μm.

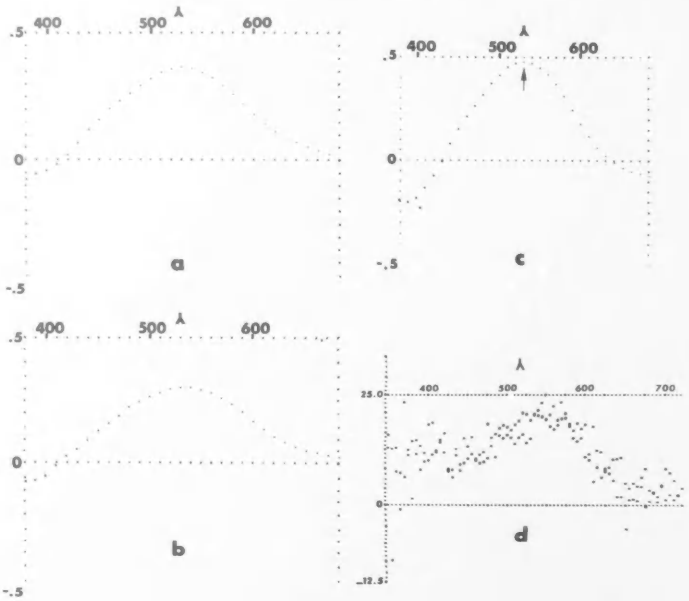


FIG. 5. a–c, Measurements of optical density (vertical axis) of retinal patches (40 μm diam) at different wave lengths (horizontal axis) in the walleye (a), sauger (b), and yellow perch (c) retinas; d, measurements of absorbance (vertical axis) at different wave lengths from an isolated rod of yellow perch.

Visual Pigments

The difference in habitat and behavior among percids, which are reflected in the organization of the visual apparatus, affect basically the sensitivity ranges of the retinas. Since the visual pigments of fishes and spectral sensitivities are known to vary with environmental light regime (Muntz 1975), in situ visual pigments in *Perca* spp. and *Stizostedion* spp., scotopic and photopic, were compared in a search for corresponding differences. Our data indicate that there are no significant interspecific differences in the absorption maxima of the visual pigments of these fishes.

The optical densities of the scotopic visual pigments of the walleye, sauger, and yellow perch retinas were measured with a spectrophotometer assembled for computer controlled microspectrophotometry (Larson et al. 1972). Measurements from a single rod, single cones, and double cones of the three species were made with a dichroic microspectrophotometer described elsewhere (Hárosi 1975).

The rods of the yellow perch absorbed maximally at about 550 nm and their photopigment is based on vitamin A_2 (Pothier unpublished data). The scotopic photopigments of the walleye and sauger absorbed maximally at about 533 and 536 nm respectively (Fig. 5a, b). Since the scotopic pigment was measured directly from isolated rods in the yellow perch only (Fig. 5d), due to the rods of the pikeperches being too slender, it is not possible to compare this aspect. However, retinal patches of the yellow perch gave maximal absorption at 530 nm (Fig. 5c) which correspond well with those of the pikeperches.

The characteristics of the cone pigments were fairly similar in the three species. Single cones absorbed maximally in the green (about 560 nm) in the yellow perch and the pikeperches (Fig. 6a, d). Both members of the yellow perch double cone absorbed maximally in the red (about 630 nm) (Fig. 6b, c); in *Stizostedion* spp. one member of the double cone absorbed maximally at about 630 nm and the other member at about 620 nm (Fig. 6e, f). In the Eurasian perch (*P. fluviatilus*) the single cones have pigment absorbing maximally at 535 nm and both members of the double cones absorbed maximally at 615 nm (Loew and Lythgoe personal communication). As the values for the Eurasian perch are averages based on a large number of measurements, the observed differences may not be significant.

Two additional observations can be made con-

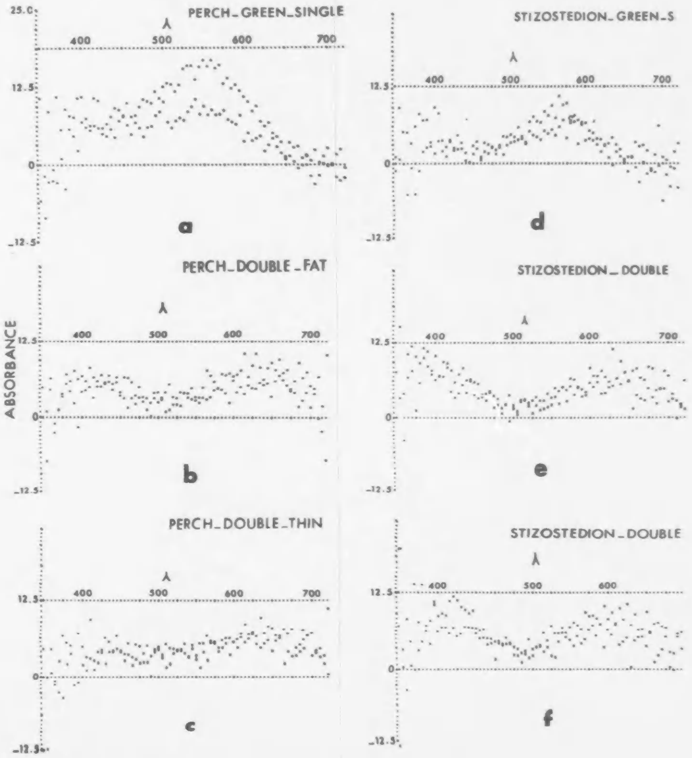


FIG. 6. Measurements of absorbance at different wave lengths from isolated cone outer segments of yellow perch (a–c) and walleye (d–f). a and d, from single cone; others, from the two elements of a double cone.

cerning these data. First, it is to be noted that no blue absorbing cones such as those reported in the goldfish (*Carassius auratus*) (Hárosi and MacNichol 1974) have been found in any of the percids studied. This is in agreement at least with the generally turbid habitat preferred by the walleye and sauger which does not transmit blue light well. Secondly, since the light reaching the rod clusters in the dark-adapted state has to be channelled first through the cone outer segments in the pikeperches, the extent to which the visual pigments of their rods and cones match may be of great consequence on the amount of useful light impinging the rods (Zyznar and Ali 1975). The green absorbing single cones of the pikeperches, for instance, are likely to produce large light losses since their pigment absorption maximum is <30 nm away from that of the rods in the spectrum. The red absorbing double cones, however, absorb far away from the absorption maximum of the rod pigments, thus allowing for only a small fraction of useful light to be lost. It is of interest, in this regard, that larger concentrations of rods are usually hanging over the double cones rather than over single cones in dark-adapted pikeperch retinas.

General Discussion

Variations in photic behavior among percids can only be accounted for by differences in the structural organization of the retinal pigment epithelium and photoreceptors, differences also expressed in electroretinographic measurements of sensitivity (Ali and Anctil 1977).

It is now generally known that adult and subadult (yearling to maturity) walleyes make crepuscular or nocturnal feeding forays on submerged boulder shoals, beds of macrophytes, or other shallow areas.

These feeding forays have been shown to be inversely proportional to ambient subsurface illumination which in turn is governed by a variety of exogenous effects including turbidity, water color, wave action, ambient surface illumination, and other factors (Ryder 1977). The sauger (*S. canadense*) has a similar bimodal feeding pattern, that of peaks during dusk and dawn (Carlander and Cleary 1949). However, as this species normally inhabits extremely turbid waters, intermittent feeding throughout daylight hours may occur because of the modified light regime created by the suspended matter in the water. Consequently, extremely high subsurface light intensities are rarely experienced by saugers in their prime habitat.

On the other hand, the yellow perch is almost exclusively a daytime feeder (Scott and Crossman 1973), although it too demonstrates a bimodal feeding periodicity with peaks during early dusk and late dawn. Hasler and Villemonte (1953) have documented diel movements of yellow perch schools from greater to lesser depths just prior to sundown where they settled upon the substrate resting upon their pectoral fins. A reverse movement took place at daybreak. Again, these movements appear to be associated with subsurface illumination.

The cooccurrence of walleye and yellow perch on shoal areas may imply the development of a closely knit symbiosis (broad sense) between these two species. In fact, the young-of-the-year yellow perch are often the largest single food item in the diet of adult and subadult walleyes (Ryder and Kerr unpublished data), a relationship that has no doubt developed by their coincidental occupancy of shoal areas during twilight periods. At this time visual performance for walleyes is approaching optimum because of morphological and physiological adaptations previously alluded to, whereas the yellow perch visual acuity is decreasing. Hence, the walleye becomes a more efficient predator concurrently and cospatially with the loss of avoidance reaction in the yellow perch, thus creating a classic predator–prey relationship. Without the characteristic photoreceptor and visual pigment differences between the two species, combined with their simultaneous occupancy of a mutually agreeable habitat at dawn and dusk, walleye and yellow perch interactions may only have been of a second order, if not mutually exclusive in time and space.

Acknowledgments

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Effects of Ambient Light Variations on Behavior of Yearling, Subadult, and Adult Walleyes (*Stizostedion vitreum vitreum*)[1,2,3]

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All facts when ordered and synthesized with previously published information suggest that light is the principal abiotic controlling variable of the environment that determines temporal and spatial dimensions of feeding and reproduction in the walleye, *Stizostedion vitreum vitreum*. Underwater observations during the day revealed that adult walleyes were active in turbid regions of a lake but rested in contact with the substrate in clear-water regions. In the latter instance physical shelter served to shield the eyes of the walleyes from the ambient light. An inverse relation was noted between numbers of walleyes sighted per hour of transect swum and transparency levels of the water. In experimental angling during the open-water season, the total number of walleyes captured and the catch per unit of effort were positively related to illuminance levels. Winter angling through the ice showed a similar relationship, though at percentage light transmission levels one order of magnitude lower. Percentages of walleyes captured per ½-h increment during openwater at dusk were positively related to percentage decrease in illuminance for the same time intervals and inversely related to absolute levels of illuminance. Other authors have determined that nuptial activity also, and hence reproduction, is governed by variations in the ambient light regime.

Key words: *Stizostedion vitreum vitreum*, walleye, light, behavior, photopic vision, tapetum lucidum, turbidity, preferred habitat, scotopic vision, feeding pattern

RYDER, R. A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1481–1491.

Toutes les observations, lorsque classées et synthétisées avec l'information déjà publiée, suggèrent que la lumière est la principale variable abiotique de l'environnement qui détermine les dimensions à la fois temporelles et spatiales de l'alimentation et de la reproduction chez le doré jaune, *Stizostedion vitreum vitreum*. Lors d'observations sous-marines diurnes, on a constaté que les dorés jaunes adultes sont actifs dans les régions turbides d'un lac, mais demeurent en contact avec le substrat dans les régions d'eau claire. Dans ce dernier cas, un abri physique sert à protéger les yeux des dorés jaunes contre la lumière ambiante. Nous notons une relation inverse entre les nombres de dorés jaunes aperçus par heure de nage sur une section et les niveaux de transparence de l'eau. Au cours d'une pêche expérimentale à la ligne pendant la saison libre de glace, le nombre total de dorés jaunes capturés et la prise par unité d'effort avaient tous deux une relation positive avec les niveaux d'éclairement. La pêche à la ligne à travers la glace en hiver montre une relation semblable, bien qu'à des niveaux de transmission de la lumière, en pourcentage, inférieurs d'un ordre de grandeur. Les pourcentages de dorés jaunes capturés, cumulés par intervalles d'une demi-heure, au crépuscule pendant la saison libre de glace ont une relation positive avec le pourcentage de diminution d'éclairement dans les mêmes intervalles de temps et une relation inverse avec les niveaux absolus d'éclairement. D'autres auteurs ont trouvé que l'activité nuptiale, et partant la reproduction, étaient également réglées par les variations du régime lumineux ambiant.

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THIS study places in perspective with previously published information the results of new observations on yearling, adult, and subadult walleye, *Stizostedion vitreum vitreum*, behavior as affected by the variations of the ambient light regime.

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New data were obtained principally from general qualitative observations of SCUBA divers, counts of walleyes by divers swimming 1-h transects, and fishing experiments that tested feeding rates at various illuminance levels.

These in situ observations complement the histological and electrophysiological studies of the retinal structures of the walleye by Ali and Anctil (1968, 1977), who concluded that they were best adapted for dim-light activity. The laboratory studies of Scherer (1971, 1976) on the photic behavior and vertical positioning of the walleye at various light intensities also support my field observations relating light intensity to walleye activity in the present study.

Materials and Methods

Most of the unquantified observations relating to walleye behavior were made by me in various Ontario lakes between 1962 and 1976 during more than 1000 h of SCUBA diving. The principal waters studied by this method were the following six lakes: Baptiste (45°07′ N, 78°02′ W), Benoir (45°11′ N, 78°09′ W), Elephant (45°08′ N, 78°08′ W), Lac Seul (50°20′ N, 92°30′ W), Minnitaki (49°58′ N, 91°50′ W), and Shebandowan (48°42′ N, 90°15′ W). In addition, four rivers were studied: the English (49°55′ N, 90°45′ W), Kashabowie (48°28′ N, 90°27′W), Shebandowan (48°42′ N, 90°00′ W), and York (45°12′ N, 78°09′ W). Occasional observations were made in more than 100 additional lakes across the province. Diving transects with standard SCUBA gear lasted approximately 1 h each and were made at practically constant depths of the littoral. All adult, subadult, and yearling walleyes seen on each transect were counted and recorded. The following notations were made for each transect: depth, presence or absence of discernible current, substrate type, degree and kind of walleye activity, approximate size of fish, and type of cover in which walleyes were observed or nearest cover when active. After each dive, transparency measurements were made with a standard (22 cm diam) Secchi disc as described by Welch (1948). Diving transects specifically for the purpose of determining the optimum transparency level for daytime activity were swum between the hours of 1000 and 1400 on sunny days only. It is expected that an optimum transparency range would be discerned empirically at which walleyes might be active at ambient daylight intensities.

Studies relating feeding periodicity to surface illumination levels were done principally in Shebandowan Lake during the open-water season and in Loggers Lake (49°53′ N, 91°44′ W) during the period of ice cover. Observations were made and data collected at an additional five Ontario lakes and streams that contributed to my overall impressions of light effects on walleye feeding behavior, but intensive studies were not carried out on these waters. Surface and subsurface illumination levels were measured with a G.M. Electrophotometer, Model 268WA300, and checked for range precision with a Norwood Director exposure meter Model M$_2$. The former instrument was equipped with a Weston Photronic cell with a spectral sensitivity of 270–750 nm (wavelength). Output was recorded as microamperes and converted to illuminance units, lumens per square metre (lux). All open-water angling took place at the same station in Shebandowan Lake, over a boulder shoal of constant depth (7 m), so that subsurface illumination was directly related to surface illumination. Frequent diving observations on this shoal substantiated that walleyes were generally present during daylight and well into dusk.

Bait-fishes used for the angling experiments were principally fathead minnows (*Pimephales promelas*), finescale and northern redbelly daces (*Phoxinus neogaeus* and *P. eos*), pearl dace (*Semotilus margarita*), and northern lake chubs (*Couesius plumbeus*). Bait-fishes were size selected for 5–8 cm total length. Angling consisted of fishing with a single minnow 0.5–1 m above the lake bottom in depths of 2–7 m. Light measurements were made at 0.5-h intervals and whenever a walleye was captured. Angling usually commenced at least 1 h before initiation of feeding in the evening, which had been previously established on the basis of 24-h fishing stations. On extremely windy days it was usually necessary to start from 0.5 to 1 h earlier, as surface agitation reflected a larger portion of the incident light and increased concentrations of suspended matter, and feeding commenced earlier. Initial fishing on a 24-h basis indicated only occasional, intermittent catches during daytime and nighttime, with the greatest concentration of feeding activity occurring at dawn and dusk. Of these two periods of concentrated feeding activity, the evening period was the most productive and further sampling efforts were concentrated there.

To better understand light–feeding relationships a "typical" conglomerate evening was composed by averaging illuminance levels at each of six 0.5-h intervals for 20 evenings during June, July and August in which there was little wind and a relatively clear (unclouded) sunset. Curves were related to a common time scale approximating mean values for the 3-mo data combined. Angling continued at least 0.5 h after the last fish was captured or until the electrophotometer recorded no further decline in light intensity (about the 4 lx level), whichever was later. Winter angling through the ice utilized the same general methodology except that several lines were fished simultaneously.

Preferred Daytime Habitat and Activity Observations

Most walleyes were observed in the portions of lakes where there was a slight perceptible current. An apparent discrepancy was introduced into the ratio of active to resting walleyes observed by the presence of the diver. Shock waves, bubbles, and regulator vibrations created a flight distance of 3–5 m between diver and fish, and many of the walleyes concealed under cover were not seen by the passing diver unless he returned to the immediate area shortly after, where he might observe a formerly "resting" walleye in the "active" state. Transects made over the littoral zones around small islands confirmed this, as the number of "active" walleyes observed was almost always markedly greater on the second circuit than on the first. This disturbance of resting walleyes by divers appeared to be more frequent in still than in turbulent waters. Consequently, the ratio of active to resting fish was disproportionately in favor of the "actives" (Table 1). Extremely cautious swimming in clear water, however, rarely revealed an active adult walleye at ambient daytime light intensities except when the skies were overcast.

Most active walleyes seen were swimming slowly away from the diver in small schools. When the diver ceased breathing and dropped motionless to the bottom, a school would file past in twos and threes about 3 m in front of the diver, making a wide circle behind him to repeat the performance. In extremely turbid waters, often the only portion of the walleye anatomy perceived by the diver was the immaculate white tip of the ventral lobe of the caudal fin. This obvious focal point in dimly lighted waters may be conceived to have survival value by allowing adult walleyes to maintain tight schools through visual perception of one another. The dull, olive-brown coloration of the walleye head, trunk, and caudal peduncle, in general, obscure them from human vision at close quarters in tannin-stained waters or those with high concentrations of suspended coloidal clays of Pleistocene lake origin.

Resting walleyes were generally partially concealed in the interstices of boulder shoals, in cover of dense beds of submersed aquatic plants or sunken trees, wood slabs, brush piles, or the various types of debris usually encountered on lake substrates. Often only the head and anterior portion of the body were hidden, the caudal portion protruding out of the cover, conspicuous again because of the white, pigmented ventral lobe of the caudal fin. Some of the resting fish, however, were more exposed, lying beside a boulder or log, or resting on beds of short-stemmed *Isoetes sp.* All resting fish appeared to be "sleeping," and their ventral regions were normally in direct contact with the substrate or the submersed macrophytes. Occasionally one of these resting fish, if carefully approached, could be touched or grasped by the caudal fin or peduncle. Resting fishes rarely returned when touched, but usually departed from the vicinity of the diver in quick erratic darts, often leaving behind "clouds" of suspended clay or organic matter disturbed in their flight.

TABLE 1. Numbers of walleyes observed during 1000 h of underwater transects in an active (swimming) mode and in a resting position. Walleyes in the resting mode were motionless and in contact with the substrate. First number in each column refers to walleyes observed in areas of perceptible turbulence, while numbers in parentheses are for those in a strictly lentic environment.

Substrate type	Active (exposed)	Resting	
		Concealed	Exposed
Boulders	1761 (19)	20 (15)	9 (1)
Other cover	1 (—)	7 (6)	1 (—)
Plants	1 (16)	5 (10)	— (3)
Total	1763 (35)	32 (31)	10 (4)

Most walleyes (98%) observed in the portions of lakes where perceptible currents existed were swimming when approached by the diver (Table 1). These areas consisted of the deltaic shallow waters off the mouths of large rivers, or the relatively turbulent waters found in the constricture of a lake such as a narrows. Where currents existed, walleyes were more easily approached, especially from the downstream direction. Hidden walleyes utilized boulders or cover of terrestrial origin for the most part, as underwater plant growth was usually sparse in these instances, especially where the current was appreciable. Schools of active walleyes often ranged from three or four associated individuals to extremely large schools. It was usually difficult to count accurately schools of more than 50 walleyes, although in some instances relatively precise numerical estimates were placed on some schools up to 150. Most schools of walleyes were oriented with their heads facing the current origin unless disturbed, whereupon they would often swim or drift rapidly downstream. Walleyes disturbed in this fashion would gradually work back to their original positions in the current or back eddy.

The major difference observed in the preferred habitats of yearling, subadult, and adult walleyes was that cover of suitable size for concealment of the small yearlings was in greater abundance than for the larger adults. A greater number of yearlings, therefore, were observed resting completely hidden under small trunks or bark where available space would be insufficient for the concealment of even the head of an adult. All three age-groups often schooled together, and observed cannibalism was usually restricted to occasional adult predation on yearlings and only rarely on other, smaller adults.

Some adult walleyes were captured, held in shallow water at ambient daytime light intensities, taken by a diver to the depth stratum at which walleyes normally occur, and released. Walleyes released in this manner invariably swam erratically at first, in quick darts, often striking underwater objects, but eventually outdistancing the pursuing diver. Where boulder shoals were available, these walleyes usually disappeared rapidly into the interstices of the boulders. It may be inferred, therefore, that acclimation to subsurface illumination levels is requisite to the effective function of vision in walleyes.

Transparency Effects

Transparency was isolated as an important variable influencing walleye behavior through observations made on SCUBA diving transects. A total of 495 active walleyes were observed during 40 h of underwater transects made specifically for this purpose. The interpretation of the resulting observations takes cognizance of the fact that the "flight distance" of active walleyes is between 3 and 5 m and therefore, like the recruitment limb of a catch curve (Ricker 1975), walleyes, on average, were not fully vulnerable to observation at distances <3 m. Hence, the ascending limb of the "sight curve" (Fig. 1) results from observations of only a portion of the walleyes actually present. Because of the bimodal form of the curve, however, it is suspected that the initial mode at 1–1.9 m might be the actual optimum transparency level for walleye activity at daylight subsurface light intensities. At this transparency level, sightings perhaps related more to the sheer abundance of active walleyes than to the diver's ability to perceive all fish present. The initial observed mode (Fig. 1) then might be considered as a "qualitative optimum," but quantitatively not proportionate to the transparency levels indicated by the remainder of the curve. The peak number of active walleyes observed (at 4–4.9 m), on the other hand, is likely to be representative of actual standing stocks, as it occurred at the upper end of "flight distance" and consequently the efficiency of diver observation approached optimum as it approached the maximum flight distance. Hence, the descending limb of the curve from apex to base (4.9–7.9 m) is truly representative of relative proportions of the standing stocks observed. In essence, the first peak represents an actual optimum transparency level favorable for walleye activity, and the second peak a combination of relatively large numbers of active walleyes and the approach of optimum visibility for the diver.

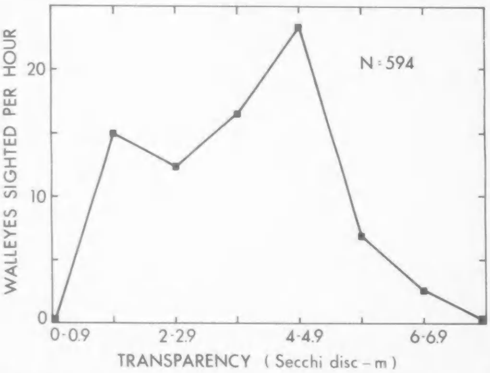

FIG. 1. Numbers of actively swimming adult and subadult walleyes sighted per hour in littoral by SCUBA divers over a range of transparency (Secchi disc) levels. Divers swam at practically constant depths and counted all adult and subadult walleyes seen. Diving for the purposes of this experiment, was done only between the hours of 1000 and 1400 on sunny days to optimize diver visibility and minimize variability of light intensity. Most active walleyes were observed in waters of transparencies ranging between 1 and 1.9 m Secchi disc (walleye preferendum for daytime activity) and 4 and 4.9 m (favorable diver visibility).

Illumination Levels and Feeding Rates

The relationship between ambient surface light intensities and feeding rates was studied during the open-water period by experimental angling and simultaneous recording of surface illumination. Analysis of 203 paired observations of captured fish and surface illuminance revealed an inverse relationship between total numbers captured and absolute levels of illumination (Fig. 2, solid curve). Of the total number of walleyes taken, 90% were captured at surface illumination levels <1000 lx and 60% at levels <400 lx. The largest single group of fish, those captured between 4 and 100 lx, constituted 40% of the total sample. Within this group, however, relatively few fish were captured below the 10-lx level. When the $\log_{10}$ of numbers of captured fish (Y) were regressed on $\log_{10}$ increments of 200 lx of surface illuminance (X), a highly significant (**) inverse relationship resulted: $Y = 44.670X^{-1.26}$; $r = -0.934^{**}$. On this basis, therefore, actual feeding rates of walleyes appeared to be related to surface (and hence subsurface) illuminance levels. The greatest feeding activity occurred at the lower illuminations.

Because of the sinusoidal pattern of diminishing light intensities (Fig. 3), catch per unit of effort was also considered at each illumination level (Fig. 2; broken line). Maximum feeding

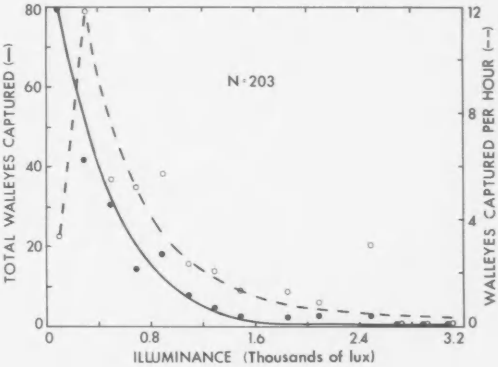

FIG. 2. Total numbers of walleyes captured by angling at dusk during the open-water period (———) and catches per unit of effort (- - - -) in relation to surface illuminance. Maximum catch per unit of effort occurred at the optimum illuminance level for feeding at 400 lx, while low catch rates were associated with high illuminance levels of from 1600 to 3200 lx.

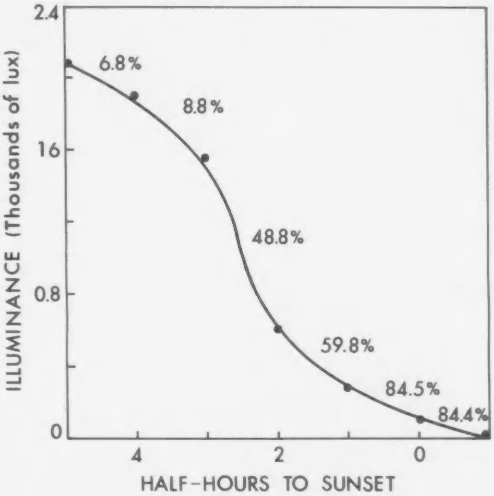

FIG. 3. Percentage rates of decrease in illuminance levels by 0.5-h intervals at dusk determined from observations made during 20 unclouded sunsets in the summer months on Shebandowan Lake (48°42′ N, 90°00′ W).

rates (CUE = 12/h) occurred at 200–300 lx and dropped off to 3.3/h at lower illumination levels. A regression of CUE from the relatively low illumination during maximum feeding rates to the highest illumination level tested showed again in a highly significant relationship: $Y = 4.520X^{-1.05}$; $r = -0.850^{**}$. Therefore, CUE of angled walleyes was inversely related to surface illumination levels from about 300 to 3200 lx, and dropped off again at levels between 100 and 4 lx. The apparent decline at lower light levels may have resulted from walleyes attempting to optimize feeding conditions by remaining at preferred light levels. They may accomplish this by moving shoreward into littoral waters or by moving upwards in the water column and feeding pelagically. Walleyes were observed to follow these behaviors for the amelioration of nocturnal feeding conditions.

The percentage rate of change of illumination was greatest in the last two 0.5-h intervals (84%) and least (7%) in the first interval (Fig. 3). The greatest absolute change in illuminance occurred in the time intervals 0.5 h before and after sunset, with the largest CUE occurring in the interval 0.5 h before sunset. Hence, the relative rate of change of illumination combined with optimum illumination levels are more important factors in providing favorable feeding conditions than absolute change in illumination per se (Fig. 4). On the other hand, the data may be indicative of an upper threshold level of illumination for feeding activity (F. E. J. Fry personal communication).

The distribution of winter catches of walleyes plotted against illuminance levels (Fig. 5) corresponded closely with data for the open-water season (Fig. 2). The range of the winter data obtained from Shebandowan Lake practically coincided with that of the summer data. The

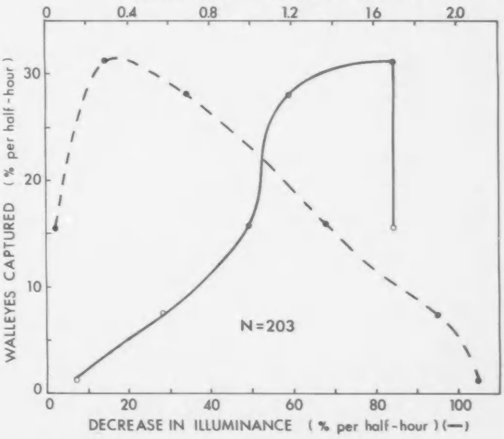

FIG. 4. Percentages of total walleye catches by 0.5-h increments at dusk in relation to absolute levels of illuminance (- - - -) and percentage decreases in illuminance (———) during each ½-h interval. Maximum catches occurred at the greatest percentage decrease in illuminance and a low level of absolute illuminance.

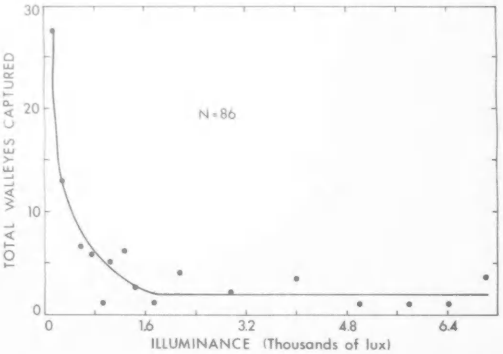

FIG. 5. Numbers of walleyes captured by angling through the ice in relation to surface illuminance at dusk and dawn. Maximum catches occurred for both periods at about 400 lx.

extension of the data beyond the 3200 lx level was mainly a contribution of the three turbid lakes (Loggers, Dinorwic, Cedar), where colloidal material in the water ameliorated the subsurface light effects and provided a longer period of favorable feeding conditions.

Most noteworthy, perhaps, was the occurrence at similar surface illuminance levels of the largest catches and also the greatest catches per unit of effort in the winter and during the open-water period. This coincidence occurred even though subsurface illumination levels beneath the ice in Shebandowan Lake were about one order of magnitude less than comparable open-water levels (Fig. 6). This observation supports my proposal that rate of change of illumination levels may be more important in stimulating the initiation of feeding than the attainment of a preferred absolute level per se. Others have also observed that the total subsurface light regimen during winter is at substantially lower levels than in the summer due to snow and ice cover (Maguire 1975a). This is a condition that persists sufficiently long (about 7 mo on the study lakes) for organisms to adapt on an annual basis to a light regime of about one order of magnitude lower than summer levels. Rapid changes in illuminance levels in winter, however, also occur at dawn and dusk, and feeding intensity tends to be related to that pattern.

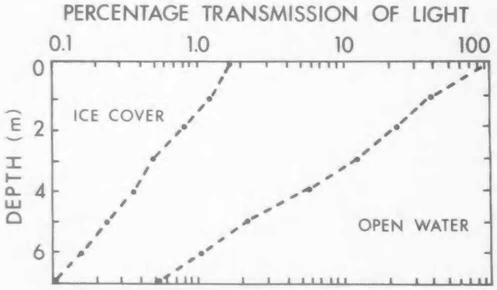

FIG. 6. Percentage transmission of light in Shebandowan Lake during maximum ice cover (March) and in midsummer (July) at depths to 7 m. Walleyes captured at 7-m depths during both seasons and at 400 lx surface illumination levels were active in subsurface illumination levels less by one order of magnitude in winter than in summer.

General Discussion

The results of my observations suggest that the diel and annual light regimes govern much of walleye metabolic activity, particularly that of feeding and reproduction. This influence on behavior is effected at each stage of the life history and is related to the development and transformation of the retinal structure. At the fry stage, the retinal response is one of positive phototaxis (Houde and Forney 1970) which changes to a negative phototactic response before the 2nd yr of life.

Many vertebrates possess a subretinal *tapetum lucidum* which improves visual efficiency under dim-light conditions (Denton 1971). This structure may not be morphologically homologous in all the vertebrate classes although the function may be similar, that is, to provide favorable visual conditions for feeding or nuptial activities during twilight or night in clear waters, or in extremely turbid waters. Potential predators or competitors lacking one or more adaptations for successful dim-light activity (e.g. tapeta, barbels, sensitive acoustico-lateralis system etc.) are normally quiescent or less active during periods of low light intensity and predation or competitive factors are reduced accordingly. Similarly, it is likely that prey species lacking adaptations for dim-light activity are more easily captured during this period when in the active mode.

The possession of a subretinal tapetum was first described for the genus *Stizostedion* by Wunder (1925a, b, 1930), who noted the presence of guanine in the pigment epithelial cells of the dorsal portion of the retina in pikeperch, *S. lucioperca*. Moore (1944) verified this condition in *S. vitreum vitreum* but noted some marked differences in retinal pigment distribution between that species and *S. lucioperca*, as reported by Wunder (1930). Because the effective area of the tapetum was greater in *S. vitreum vitreum*, Moore concluded that that species was better adapted than *S. lucioperca* for scotopic (dim-light) vision. Conversely, *S. lucioperca* was not as committed to dim-light activity as *S. vitreum vitreum*, although it was generally crepuscular or nocturnal in behavior. More recently, Ali and Anctil (1968) have shown that sauger, *S. canadense* is probably the genus representative best adapted to dim-light activity, as several retinal characteristics favor scotopic vision (Ali and Anctil 1977). Subsequently, Ali et al. (1977) have proposed the existence of a symbiosis (broad sense) between *S. vitreum vitreum* and one of its principal prey species, yellow perch, *Perca flavescens*. Here, increased visual acuity of *S. vitreum vitreum* during twilight periods coincided with the decreasing efficiency of the photopic vision of *P. flavescens*. Hence, the coexistence of these two species in the shallows at twilight, coupled with the inverse complementarity of their respective visual apparati, allowed *S. vitreum vitreum* to become a more efficient predator concomitantly with a decreasing avoidance reaction of *P. flavescens* which made the latter species more vulnerable to predation.

Young-of-the-year walleyes were found to be positively phototactic at ambient daytime illumination levels from the time of hatching through the post-larval stage (Houde and Forney 1970). In this instance they frequented the limnetic zone and fed pelagically, for the most part, on zooplankton. While in this stage they may be attracted to the surface waters at night by the use of an artificial light (Regier et al. 1969). Houde (1969) considered that increases in abundance of walleye larvae at the surface during nighttime may have been a photopositive response to bright starlight. Post-larval walleyes 2.5–3 cm long frequented the littoral and were sometimes found nearshore in shallow sheltered bays. Presumably this change in habits reflects the transition period between the positive phototactic response during early life and a negative phototaxis at older ages. Post-larval walleyes gradually move from the littoral shoals into deeper water as summer progresses (Raney and Lachner 1942), indicating a continuing adaptation to progressively decreasing light intensities, or conversely, an avoidance of high daytime illumination levels.

Yearlings, subadults, and adults are aggregated in this study, as the diving observations showed that complete negative phototaxis at daytime illumination levels was acquired before the 2nd yr of life (R. A. Ryder diving records). Thus, these three age categories react almost uniformly in movements and feeding behavior under various light intensities, with only adults responding differently during the spawning period. Eschmeyer (1950) recorded daytime spawning of walleyes as a rare occurrence at Lake Gogebic. He observed that spawning occurred almost exclusively at night and was difficult to observe because of the negatively phototactic response of the fish to artificial lights. Walleyes, however, often remain on the spawning grounds during daylight hours, although vigorous prenuptial activity and discharge of the seminal products occur only at substantially lower light intensities (e.g. Ellis and Giles 1965). Possibly, as walleyes approach spawning condition, negative phototaxis is partially masked through hormonal changes initiated by photoperiodic control. Consequently, spawning walleyes may show relatively less negative response to bright artificial light than those engaged in prenuptial activity. This decreased negative response occurs for about 1 wk after completion of spawning and is usually observed by the angler in the form of extremely good fishing in shallow waters close to the spawning grounds during daylight hours immediately after the eggs have been deposited. Hence, the light effect coupled with the postspawning physiological need for food usually provides ideal angling conditions. This effect may be magnified in turbid waters and the successful fishing period extended accordingly.

Other authors have made observations during the walleye spawning period at various light intensities. Ellis and Giles (1965) have observed nuptial activity to remain at a low level during daytime and consisted primarily of position holding. Increased courtship behavior occurred as the level of illumination dropped in the evening. In an artificial compound spawning acts occurred most frequently at a declining surface illuminance of 2800–750 lx, which was noted to be a slightly higher level than that for wild fish.

Effect of light on movements — Walleyes, because of their sensitivity to high illumination levels, are more likely to search for food at twilight or night than on sunny days. This mobility makes them more vulnerable to capture by gill nets at night as shown by Carlander and Cleary (1949). Gill nets set in deep and shallow water in Lake of the Woods indicated not only more walleye movement by night but also a shoreward movement of the fish into the shallows, presumably to feed. Similar observations at Clear Lake, Iowa, suggested that the greatest periods of mobility were dusk and dawn. During two days on Lake of the Woods, a rain shower and darkening of the sky occurred with a corresponding increase in numbers of walleyes captured. Carlander and Cleary (1949) suggested that these data indicated a close relationship between diel walleye movements and light intensities. Deeper gillnet sets for walleyes indicated less diel variations in movement than was found for the shallower sets. Presumably, walleyes in deep water are closer to optimal levels of illumination for metabolic activity such as feeding and are more active during the daytime than those in shallow waters. As the light regime is more nearly uniform in the greater depths and extremely turbid waters, rates of change in surface illumination may not have as great an effect in the stimulation of feeding as it does in shallow or clear waters.

Factors that influence illumination levels — The reaction of the walleye to various levels and changes in level of illumination greatly influences its mode of life. To predict these effects it is necessary to understand those factors that generate changes in subsurface illumination as experienced by the fish. These factors can be broadly grouped into three major categories: celestial, meteorological, and limnological. Each is interrelated to some extent and either ameliorates or reduces light levels between the source and the walleye retina. Within each category are physical, chemical, or biological components that individually influence the subsurface illumination. The sun (moon, stars) provides the light source, and the meteorological and limnological effects serve to attenuate it until the illumination that eventually reaches the retina of the fish is only a small fraction of the initial radiant energy.

Besides providing the light source, the sun also affects light intensity on a diel and a seasonal basis. A change in altitude from the noon position results in more reflection of incident light rays by the water surface, and less absorption occurs. Similarly, less surface incident light is generated at noon in December than for the same time in June in the northern hemisphere.

Direct meteorological effects shield or screen the sun's rays from the water surface. Cloud cover alone, or cloud cover combined with precipitation in the form of rain or snow, may decrease illumination levels markedly. Precipitation has a secondary effect of disturbing the water surface, thereby creating a turbulent condition which reflects more light and absorbs less.

Winter precipitation in the form of snow or sleet settles on a permanent ice cover and effectively reflects a major portion of incident radiation (Maguire 1975a, b). Wind velocity and direction are also important considerations in evaluating subsurface illumination. Wind creates waves, which reflect or absorb light, and increases turbidity by increasing the quantity of suspended material in the water.

Limnological effects on light intensity may also be physical, chemical, or biological in nature. Changes in transparency may be either spatial or temporal and are affected by water flow, waves, and thermal or chemical stratification. Changes in turbidity and true color affect transparency and in themselves may be affected by organic or inorganic sources. The formation of winter ice cover on a lake drastically reduces light absorption depending on the quality of the ice (translucent or opaque). Algal blooms and zooplankton concentrations are also often important factors in the attenuation of incident light.

General reactions of walleyes to illumination flux — The greatest effect on walleye behavior created by different levels of illumination is generated by (1) variable transparency levels within and between lakes and (2) the diel light cycle.

That walleyes in waters of low transparency are more inclined to feed intermittently throughout daylight than those in clear lakes is well known to most ardent anglers. In Shebandowan Lake this observation was confirmed when comparing the turbid region off the mouth of a large tributary river (Secchi disc 3 m) with the clearer waters of the lake proper (Secchi disc 5.5 m) and is aptly demonstrated by the activity levels shown in Fig. 1. Lakes with the highest standing crops of walleyes (Elsey and Thompson 1977) in northwestern Ontario are usually large lakes with rather concentrated organic suspensions, often tannin stained, and with a transparency level of about 1 to 2 m (Secchi disc). Lakes lying on the old lake bed of Pleistocene Lake Agassiz are also frequented by walleyes; their high turbidity results from colloidal clays of glacial origin and provides adequate screening from high illumination levels even in shallow water. In a similar environment, Wunder (1930) found that 6 out of 37 species (including *S. lucioperca*) known to occur in Lake Balaton had tapeta and he concluded that these species were more successful in this extremely turbid lake than those lacking this structure.

Clear lakes, on the other hand, may produce many walleyes; but the standing crops are usually substantially less than lakes of low transparency. This is probably caused not only by the lower nutrient levels usually associated with clear lakes but also by the restriction placed on the length of time that optimum levels of light for feeding are available to walleyes. Unless dense cloud cover, heavy precipitation, or high winds reduce the ambient illumination, walleyes are rarely captured by angling in clear lakes during daylight except at great depths. Most feeding by walleyes in clear lakes is either crepuscular or nocturnal, the scotopic vision being of substantially greater value in this respect than photopic vision. Walleyes optimize daytime light levels by (a) swimming to deeper water and using the vertical stratum of water as a light filter, (b) swimming to a more turbid (and usually turbulent) portion of the lake, or (c) by remaining in shallow water and utilizing some form of physical shelter, such as boulders or weed beds, to shield themselves from the high subsurface light levels (R. A. Ryder diving notes). While walleyes make use of all three methods to avoid unduly high illumination levels, the latter method is more commonly employed, providing that shelter is readily available.

Illumination levels and photoperiodic response — The photoperiodic response in walleyes is geared to diel and seasonal changes in light intensity. An inherent circadian rhythm also governing feeding times (e.g. Aschoff 1960; Kalmus 1966) is likely modified by the photoperiodic effect on feeding times. Laboratory studies in which walleyes could be fed under controlled environmental conditions might solve the problem of whether feeding is stimulated primarily by endogenous or exogenous factors. However, in a highly photonegative fish such as the walleye the exogenous light factor seems to be more significant in initiating the movement that subsequently results in feeding. This occurs upon attainment of illumination levels suitable to scotopic vision. These levels are attained normally twice during a 24-h period, at dawn and at dusk. Seasonally these periods become altered as daylight attenuates and the nights lengthen with the approach of winter. The walleyes' feeding times are altered accordingly to remain in harmony with the twilight periodicity. Hence, winter feeding under ice and snow cover occurs at about the same surface illumination levels but at substantially lower subsurface intensities. Consequently, the rate of change of illumination is the major factor that stimulates the initiation of feeding once appropriate levels of illumination are achieved (or a threshold level is reached). Additionally, an adaptation to the lower winter light regime occurs such that optimal level of illumination required for efficient feeding is one order of magnitude or more lower than corresponding open-water levels.

The major exogenous stimulus that initiates feeding in all seasons is the decline of the sun below the horizon (Fig. 2 and 3) or the ascent toward the horizon. These conditions create disproportionately large changes in subsurface illumination levels as the luminous flux is reflected through sky light and none is transmitted directly to the water. Blaxter (1966) noted that feeding incidence of visual feeders usually started to decline at a relatively high light intensity, but perhaps fell to zero only after a reduction of 0.001–1.0% of the initiation level. Though 300 lx was the optimum or threshold level for feeding in the walleye (Fig. 2), cessation of all feeding did not occur until the surface illumination fell considerably below 5 lx or at least to 1% of the threshold level. Walleyes prolong optimum light levels for feeding by moving into shoal areas or becoming pelagic as evening progresses. This supposition was verified by moving fishing stations from the 7 m depth 0.5 h following cessation of feeding to stations 1–2 m in depth, whereupon fish were again captured. This observation is not inconsistent with a preferendum theory whereby fishes or other organisms move upwards in the water column with declining light intensity in the evening (Blaxter 1975). Ringelberg (1964), on the other hand, concluded that vertically migrating organisms responded not primarily to the necessity for maintaining a light preferendum but rather to the rate of change of light intensity. The results of the present study indicated that the two considerations are about equally important in governing walleye movements, and hence, feeding rates.

Initial experiments with photometric readings at depths to 7 m with the instrument available showed a lack of sensitivity to changes in subsurface illuminance levels to which the walleyes responded readily. With decreasing surface illumination levels, subsurface levels are reduced proportionately less because of the greater reflection of light as the angle of incidence increases. It is noteworthy, therefore, that walleyes feeding at 7 m depths respond so readily to minute subsurface changes in illuminance. They are almost certainly aided in this respect by their well developed subretinal tapeta and other retinal characteristics (Ali and Anctil 1977), which provide them with crepuscular and nocturnal feeding capability not afforded their relative, the yellow perch, *P. flavescens* (Ali et al. 1977). Welch (1952) noted that dawn and dusk are virtually absent in water; it is therefore all the more remarkable that the sensitive visual apparatus of the walleye not only distinguishes these major periods as temporal optima for feeding and spawning, but also stratifies the twilight zone itself into smaller segments for greater or lesser metabolic activity (Fig. 2 and 4).

Other environmental variables — In discussing the effects of light on walleye behavior, I have assumed up to this point that other environmental variables, such as temperature and dissolved oxygen, fell within the range required for normal metabolic activity. Scherer (1971) has substantiated this assumption in laboratory experiments in which walleyes were subjected to changes in illumination, dissolved oxygen, pH, and free carbon dioxide levels. He found that the negative phototactic response was largely dependent on the given respiratory situation; i.e. during oxygen depletion or free carbon dioxide buildup, the response diminished to the point of obliteration, which occurred at levels that left mobility and equilibrium of the test specimens intact. When oxygen, free carbon dioxide, pH, and temperature were held constant (at a level compatible with normal fish activity), then the vertical position of walleyes was inversely related to light intensity (Scherer 1976).

In conclusion, the annual and diel light regimes constitute the major abiotic influence in the regulation of the diurnal feeding behavior and annual reproductive behavior in adult walleyes (present study; Ellis and Giles 1965; Scherer 1971, 1976). While adverse illumination levels would rarely be a direct cause of walleye mortality in natural lakes, unfavorable light regimes could contribute to feeding inefficiency, lack of effective reproduction, or higher rates of predation. Conversely, the ability of walleyes to function effectively at low levels of illumination provides the species with survival advantage by reducing competition for food and predation by day-feeding fishes. The efficiency allows adult walleyes to occupy space not utilized by feeders with photopic vision at a time when the latter are inefficient and usually dormant. This successful partitioning of a lake into time and space by this species for their own activities largely explains the high degree of success of reinvading walleyes following Wisconsin glacial recession in the face of a flock of rather efficient, large, and competitive predators, including especially *Esox lucius*, *Lota lota*, *Micropterus dolomieui*, and *Salvelinus namaycush*.

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Sensory Organs of the Lateral-Line Canal System in Two Percids and Their Importance in Behavior[1]

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DISLER, N. N., AND S. A. SMIRNOV. 1977. Sensory organs of the lateral-line canal system in two percids and their importance in behavior. J. Fish. Res. Board Can. 34: 1492–1503.

The early development of the lateral-line systems in Eurasian perch (*Perca fluviatilis*) and the ruff (*Gymnocephalus cernua*) is described and related to development of behavior patterns characteristic of the two species. Perch are active pelagic predators for whom vision is of greatest importance in obtaining food, whereas ruff are benthophages of slow-flowing waters and typically obtain their food as solitary ambush predators for whom the highly sensitive lateral-line system is extremely important. The less developed system of the perch seems to match its greater ecological plasticity.

Key words: Percidae, *Perca*, *Gymnocephalus*, lateral line, development, behavior, sensory organs

DISLER, N. N., AND S. A. SMIRNOV. 1977. Sensory organs of the lateral-line canal system in two percids and their importance in behavior. J. Fish. Res. Board Can. 34: 1492–1503.

Nous décrivons les premières phases du développement du réseau de la ligne latérale chez la perche eurasienne et (*Perca fluviatilis*) et la perche goujonnière (*Gymnocephalus cernua*) et l'associons au développement des modalités de comportement caractéristique des deux espèces. La perche aurasienne est un prédateur pélagique actif pour lequel la vision est de la plus grande importance pour la capture de la nourriture, alors que la perche goujonnière est un benthophage d'eaux lentes qui, typiquement, se procure de la nourriture comme prédateur solitaire à l'affut et pour lequel une ligne latérale grandement sensible est extrêmement importante. Le réseau moins bien développé de la perche eurasienne semble aller de pair avec sa plus grande plasticité écologique.

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THE lateral-line system in European percids has received more study than that of any other teleost family (Disler 1950, 1971; Jakubowski 1963, 1967). This has enabled Jakubowski (1967) to relate the morphology of these organs to the mode of life in different species.

The Eurasian perch (*Perca fluviatilis*) belongs to a group of active pelagic predators and rheophilous benthophages, including *Stizostedion* and *Zingel*, which are characterized by a rather high growth rate and by a considerable size. In the adult individuals of this group vision is of the greatest importance in obtaining food, the role of the lateral-line canal system appearing to be insignificant. The canals on the head of these species vary in width and configuration. However, their common property is the ossification of the external walls.

In contrast, the ruff (*Gymnocephalus cernua*) belongs, with *Percarina*, to a second group which are poor swimmers and comprise small benthophagic dwellers of stagnant or slow-flowing waters. In the members of this group the external walls of the head canals are skin membranes stretched on bony bridges situated over the neuromasts (Jakubowski 1967). The lateral-line system of these species is distinguished by a high sensitivity important in obtaining food and detecting predators.

The purpose of this paper is to describe the ontogenetic changes in the lateral-line systems of the perch and ruff and the changes in the behavior and responses of their embryos, larvae, and fry. The approach extends our previous studies (Disler 1950, 1971; Smirnov 1969, 1975).

Materials and Methods

Fertilized perch eggs were obtained from Glubokoe Lake (Moscow region). Some of the eggs were in-

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cubated in glass vessels 35 cm in diam with a water layer 10–12 cm deep, the remainder being transported to small natural ponds where the larvae turned to active feeding with greater success. Mature ruff spawners were caught with a gill net in Glubokoe Lake. The eggs, fertilized by the "dry" method, developed in vessels similar to those used for the perch eggs. The fry were grown in table aquaria of various sizes.

The morphology of the lateral-line organs was examined under a light microscope after vital staining with methylene blue. Drawings were made from live specimens with the help of a *camera lucida*. For histological examination, the material was fixed in Bouin's solution, 6–8-μm paraffin sections being stained after Mallory or with Heidenhain's Azan. Histological sections of dated material on perch development were donated by E. N. Dmitrieva.

Other samples were fixed with osmium tetraoxide after Palade (1952) or after Millonig (1962) in an ice bath for 40–50 min, and were embedded in Araldite. Sections 200 Å thick were obtained with the help of glass knives in an LKB 8800 microtome and were stained with uranyl acetate and lead citrate after Reynolds (1963). Photomicrographs were made with a JEM-7A electron microscope (Cambridge Stereoscan II) the samples were fixed after Palade, washed in 0.1 N HCl solution to eliminate the cupula, dehydrated in alcohols, and coated with gold in a vacuum evaporator.

Results

Eggs and embryos — Perch eggs without membrane are 0.91–1.00 mm in diam. The embryos are 6.3–6.7 mm long on hatching, having an elongated yolk sac with a large fat droplet (Fig. 1A). This droplet serves not only as a nutrient storage but also as a hydrostatic organ. Thanks to the fat droplet and vibrating motion of the pectoral fins, the embryos can maintain themselves in midwater. The operculum does not yet fully cover the gill arches and already visible gill filaments, but moves synchronously with the mouth motions. The eyes are pigmented, but immobile. The olfactory fossae are round, and the auditory vesicles are divided into chambers and contain two otoliths.

In newly hatched embryos the primary neuromasts are differentiating from their epidermal anlagen. The development of these anlagen from the auditory placodes and their proliferation can be seen before hatching. The better-differentiated neuromasts stain with methylene blue solution; others appear to be colorless tubercules on the surface of the body (Fig. 1). Twelve organs differentiate from the lateral rudiment which is associated with the ganglion of the Xth cranial nerve. On one head a total of 22 neuromasts differentiate from the anlagen of the supra- and infra-orbital, operculo-mandibular and temporal organ groups associated with the placodes of the VIIth and Xth cranial nerves.

At this stage of development, endogenous feeding of the embryos is still evident. With continuous vibrations of the pectoral fins and tail, they move slowly in midwater, sinking to the bottom at times.

In the water the head of the embryos is higher than the tail due to the buoyant fat droplet in the anterior part of the body and to the manner of pectoral fin motion. The embryos are not pigmented and therefore, are not easily seen in the water. Immediately after hatching they are very sensitive to tactile stimulation. During the first hours of life outside the membrane, the response to these stimuli is nondifferentiated and negative. If a circulatory water flow is created in the aquarium the embryos maintain themselves head to the current. The embryos do not have objective vision yet. However, they show a pronounced light response.

Ruff eggs are somewhat smaller than those of perch, their diameter without membrane being 0.79–0.97 mm. At similar temperatures, hatching occurs 3–4 days earlier than for perch and at a less-developed stage, since development proceeds near or at the bottom where oxygen content is lower than in midwater where perch eggs develop. The newly hatched embryos are 3.5–3.9 mm long. The yolk sac is oval with a large fat droplet in the anterior part. The pectoral fins are rudimentary. The mouth and gill apparatus are nondifferentiated. Eye pigmentation is hardly visible. The lateral-line organs are represented by anlagen proliferating in the epidermis (Fig. 1B). Most of the time the embryos remain on the bottom, where they lie on their sides, occasionally swimming up into the water column only to sink to the bottom again. They fail to respond to current and turbulence in the water but do respond to tactile stimuli to which they show a marked motor reaction. After 3–4 days, the embryos are 4.5–5.0 mm long. Both in structure (Fig. 1C) and in behavior, they are then similar to the newly hatched perch embryos.

The initial stages in the formation of primary neuromasts from anlagen are very similar to those in the perch. Cellular aggregations remaining in the areas of anlagen proliferation consist of poorly differentiated round cells, which gradually acquire the specific properties of sensory and supporting elements of the neuromasts.

The developed primary neuromasts lie in the epidermis, protruding slightly from its surface (Fig. 1D, E). A small, rod-like cupola is clearly visible in live or osmium-fixed material. The

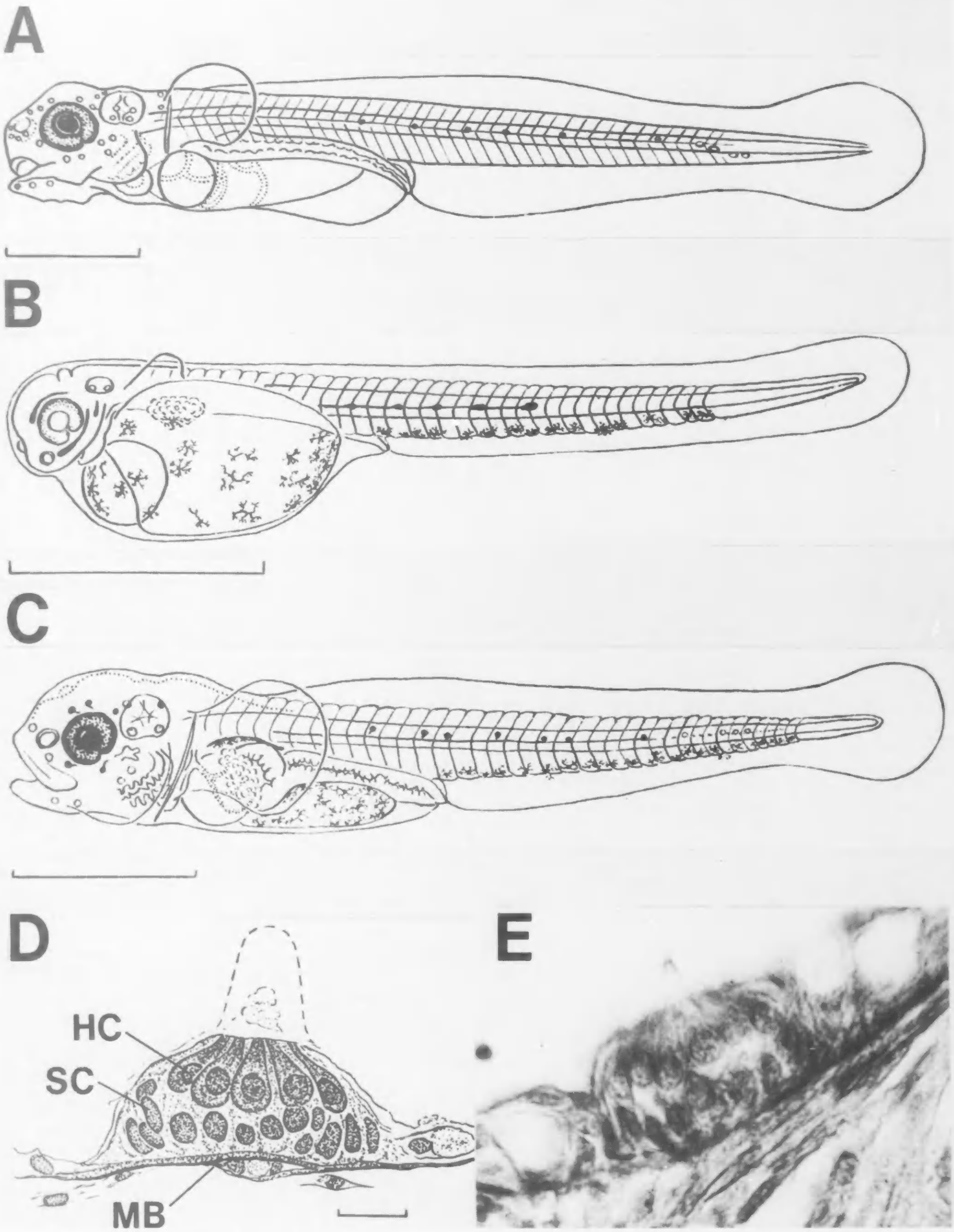

FIG. 1. Morphology of perch and ruff free embryos and their lateral line organs. A, Perch immediately after hatching, 6.7 mm long; B, Ruff at hatching, 3.6 mm long; C, Ruff 5 days after hatching. The scale shown for all three equals 1 mm. Methylene blue staining neuromasts shown as solid dots, those not taking stain as open dots. D, Primary neuromast of the supraorbital row, perch; E, Analogous neuromast, ruff. The scale in D equals 0.01 mm. HC — hair (sensory) cell; MB — membrana basalis; SC — supporting cell.

sensory cells, numbering 15–20, are typically pear-shaped. Their large, round nuclei, which take up nearly the entire width of the cells, are somewhat shifted toward the bases. The supporting cells underlying the sensory cells have elongated oval nuclei disposed below the sensory cell bodies. The apical protrusions of supporting cells which separate the adjoining sensory cells from one another reach the neuromast surface. The mantle zone, i.e. the supporting cells lying around the sensory ones, is poorly developed, there being only 2–3 cells in the cross sections.

An electron microscopic examination of primary neuromasts in ruff embryos just before the onset of active feeding has shown that both supporting and sensory cells have acquired a number of structural properties characteristic of the cells of mature neuromasts and essential for performing their specific function. However, these properties are developed to a lesser extent than in adult organs, being still in the process of formation. In fact, the hair apparatus of the sensory cells is represented by a bundle of stereocilia and by a single kinocilium. However, agglutination of stereocilia is often apparent (Fig. 2A). Microtubules, characteristic elements of the cell supranuclear region, occur in large numbers: however, they are oriented in different directions, giving an impression of irregular arrangement. Evidently, their formation is still going on, the main role being played by the plasma membrane of the lateral walls of the cell and also by some special structures of the desmosome type at its surface (Fig. 2A). The subnuclear zone, containing few organelles, is filled with various-sized vesicles scattered in clusters of 5–10 ribosomes in some sites and also by rare mitochondria (Fig. 2B).

Numerous nerve terminals contact the basal part of the sensory cell. The synaptic apparatus has been developed. However, the presynaptic bodies of the afferent synapses have a low electron density, appearing to be immature (Fig. 2B).

The basal parts of the supporting cells between the basal membrane and the sensory cells are almost fully taken up by the large nuclei. A rough-surfaced endoplasmic reticulum is still poorly developed (Fig. 2C). In the supranuclear region of these cells the Golgi complexes are formed and later develop greatly. The out-growths separating the adjacent hair cells are very thin; however, their apical parts already contain medium-sized secretory granules, their content having different electron densities.

Larvae — Perch embryos show considerable changes in morphology and behavior 1–1.5 days after hatching. The eyes become mobile and peristaltic motions of the intestine occur. The embryos react to small planktonic organisms moving in the water, pursue and catch them. With the onset of active feeding, the larval period of development begins. Both endogenous and active feeding continues about 4 days at 18–20°C. In larvae 8–9 mm long, the yolk sac and the fat droplet are resorbed and gas appears in the swimbladder. Gill filaments become differentiated to a greater extent and the gill covers enlarge. The shape of the nonpaired fin fold changes, the auditory capsules enlarge, their shape changing — the bases flatten and the apices elongate dorsally. The posterior otoliths enlarge compared with the anterior ones. The olfactory fossae become elongated. Gustatory buds develop in the mouth cavity and on the jaws. The diet of larvae of this size consists of nauplii, copepodite stages of copepods, diatoms, rotifers, and flagellates.

The lateral-line organs continue differentiation. The row of trunk neuromasts shifts dorsally above the chord level. On the head, a number of new organs appear (Fig. 3A, C). The nerves branching off from the neuromasts can be demonstrated with methylene blue at this stage. Under natural conditions, to this stage, the larvae dwell in the open part of the lake, to which they are perhaps brought by wind-driven currents (Nordqvist 1914). Subsequently, the larvae return inshore with some of them preferring the lower layers of the water.

Ruff larvae attain a morphological condition similar to that of perch at a smaller length, 6.3–6.5 mm (Fig. 3B). In contrast to perch larvae, they have no pelagic stage. The onset of active feeding and the later transition to exclusive exogenous feeding occur in the benthopelagic water layers. These observations of ruff larvae kept in the aquarium are supported by the fact that in the lake larvae are not caught by plankton nets. Generally, under natural conditions ruff larvae and fry are observed very rarely because of their secretive behavior.

As in perch larvae, the number of primary neuromasts of different groups increases in the lateral-line organs. The sensory organs that appeared earlier change somewhat, becoming lentiform due to an increase of the marginal supporting cells which form the mantle zone (Fig. 3D). The number of sensory cells in an individual organ and their structure do not change much.

For both perch and ruff larvae mobility and maneuvering capacity increase with the appearance of gas in the swimbladder. Their sensitivity to the motion of various objects in the water also increases greatly. The escape response and coordination of movements are so high that the larvae can hardly be caught with a landing-net. Observations and experiments involving presenta-

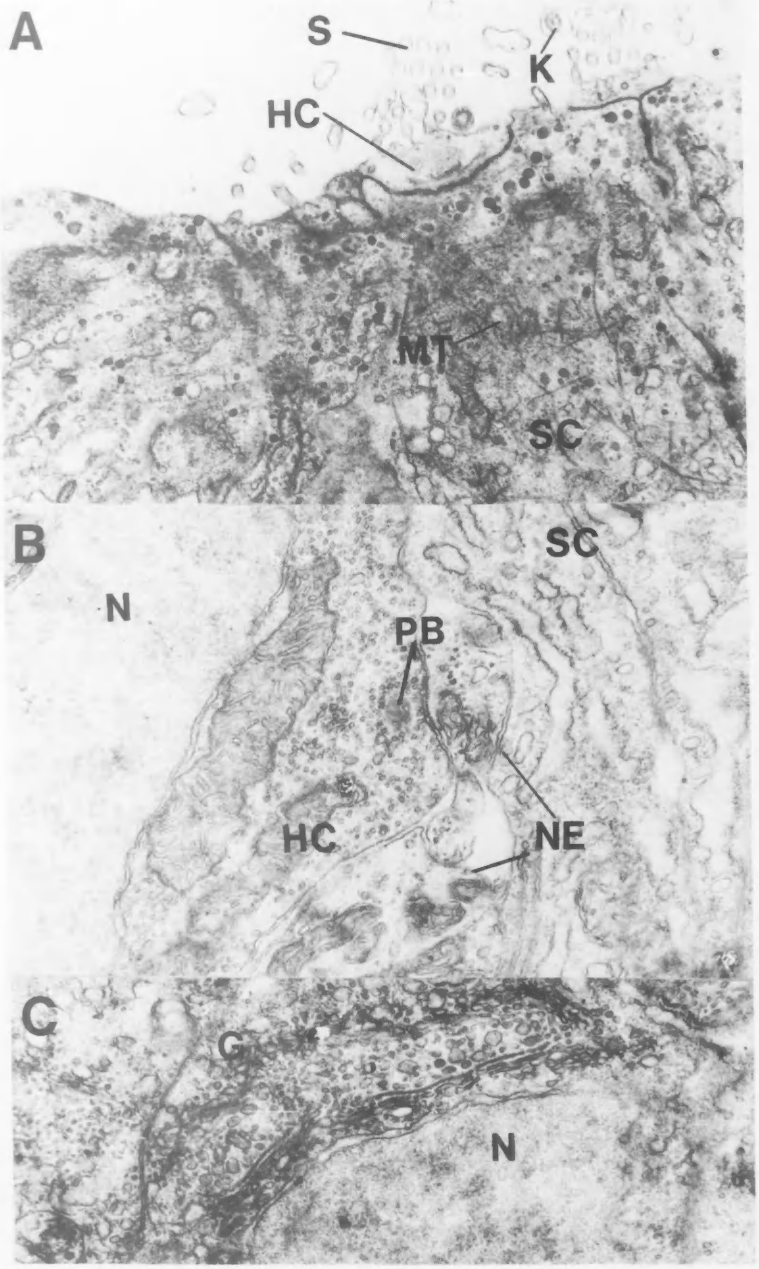

FIG. 2. Ultrastructure of a ruff primary neuromast. A, Apical part of the organ, ×9450; numerous microtubules in supporting cells and fused stereocilia can be seen; B, Basal part of sensory (hair) cell with adjacent nerve endings, ×29,400; C, Young supporting cell with intensively developing Golgi complex, ×28,000; HC — hair (sensory) cell; SC — supporting cell; G — Golgi complex; K — kinocilium; MT — microtubules; N — nucleus; NE — nerve ending; PB — presynaptic body; S — stereocilium.

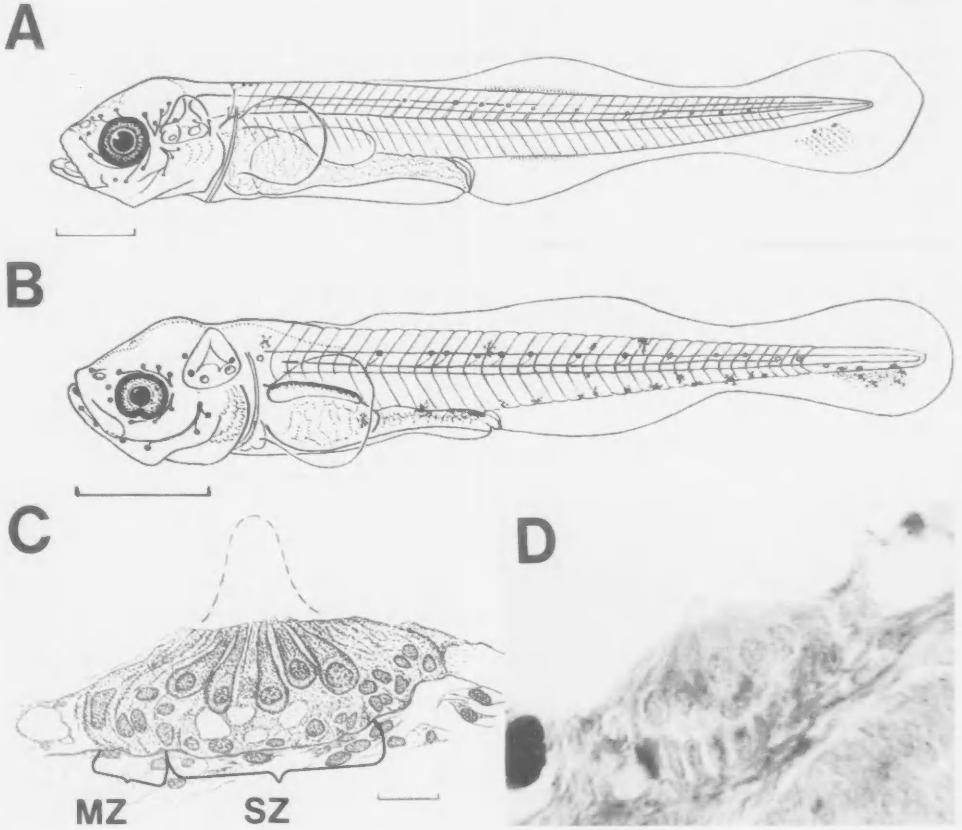

FIG. 3. Morphology of perch and ruff larvae. A, Perch 6 days after hatching, 11 mm long; B, Ruff 12 days after hatching, 6.5 mm long; C, Neuromast of supraorbital row, perch larva; D, Analogous neuromast, ruff larva. Scales shown in A and B equal 1 mm, that in C 0.01 mm. MZ — mantle zone, SZ — sensory zone.

tion of food objects through a thin glass reveal that the larvae of both species hunt with the help of vision, spotting prey at a range of 7–8 mm. Experiments show an optomotor reaction in the larvae at this stage.

At subsequent stages of the larval period considerable changes in the structure of all the organ systems and in behavior are noted. In perch larvae 10–19 mm long, rays gradually develop in paired and nonpaired fins (Fig. 4A), and the preanal fin fold disappears. Gills are differentiated and rays appear in the branchiostegal membrane, definitive respiration mechanisms being established (Personalnaya 1946). In the inner ear, ampulae are formed at the terminals of semicircular canals. On the jaws, teeth are differentiated. From the posterior part of the esophagus, the stomach develops; the shape and size of the swimbladder change, providing still better larval mobility. The larvae are capable of performing more complex motions vertically and horizontally. From the middle of the larval period onward, perch form small schools. They also feed on larger prey, mainly *Diaphanosoma brachiurum* and *Eudiaptomus graciloides* showing a high degree of selectivity (S. A. Smirnov unpublished data). Ruff larvae do not form schools when kept in an aquarium and are evidently solitary in natural conditions. In search of food, they swim over the bottom of the aquarium, and when frightened sink down quickly and take shelter. Their light response is positive, as previously.

Sensory organs of the lateral-line canal system undergo considerable changes as well. Concurrent with the continuing differentiation of primary neuromasts originated from the placode material, secondary sensory buds appear (Fig. 4A, B). As was demonstrated by Disler (1950,

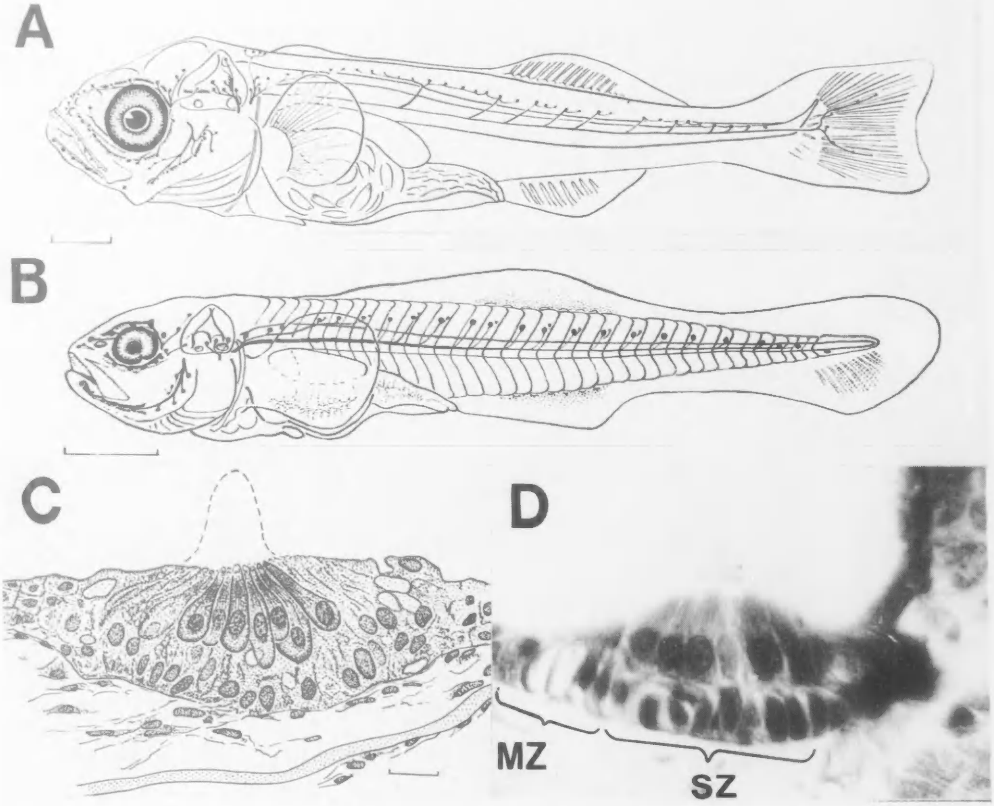

FIG. 4. Morphology of final stage perch and ruff larvae. A, Perch 12 days after hatching, 14 mm long, onset of canal formation; B, Ruff 20 days after hatching, 9 mm long; C, Neuromast of supraorbital row, 14-mm perch larva; D, Analogous neuromast, ruff larva. Scales and abbreviations as in Fig. 3.

1971) in perch, they develop from the epidermal stratum basale cells under the influence of the lateral-line nerves. The mechanism of their formation is thus similar to that found in Cyprinidae (Bailey 1937). The development of secondary neuromasts becomes possible after formation of a multilayered epidermis with a highly developed stratum basale. The numbers of these organs in perch and ruff larvae at comparable developmental stages are similar.

Further differentiation of primary neuromasts in perch and ruff larvae occurs approximately in a similar manner. The number of sensory cells increases little. However, an extensive proliferation of neuromasts due to development of wide mantle zones (Fig. 4C, D) begins. Those organs first differentiated from the anlagen increase in size. Therefore, the neuromasts of various parts of the head canal differ considerably in size depending on the time of development.

By the end of the larval period, on the heads of perch and ruff larvae, lateral-line canals begin forming; they initially have the appearance of grooves with primary neuromasts on their bottoms. Soon, over the larger earlier formed neuromasts, the edges of the grooves fuse, although the neighbouring organs are still on the body surface.

The lateral-line sensory organs appear to play a greater role in feeding at this stage. In fact, blinded perch larvae perceive vibrations produced by a water flea at a range of 2–3 mm.

Fry — In perch the fry period may begin at different times, depending on environmental conditions for example, in Glubokoe Lake, 35–40 days after hatching: in isolated ponds, 13–18 days earlier. By that time, the fry are 19–29 mm long (Fig. 5A), the second dorsal, caudal and anal fins have differentiated and the preanal fin fold has disappeared. In the abdomen, pyloric

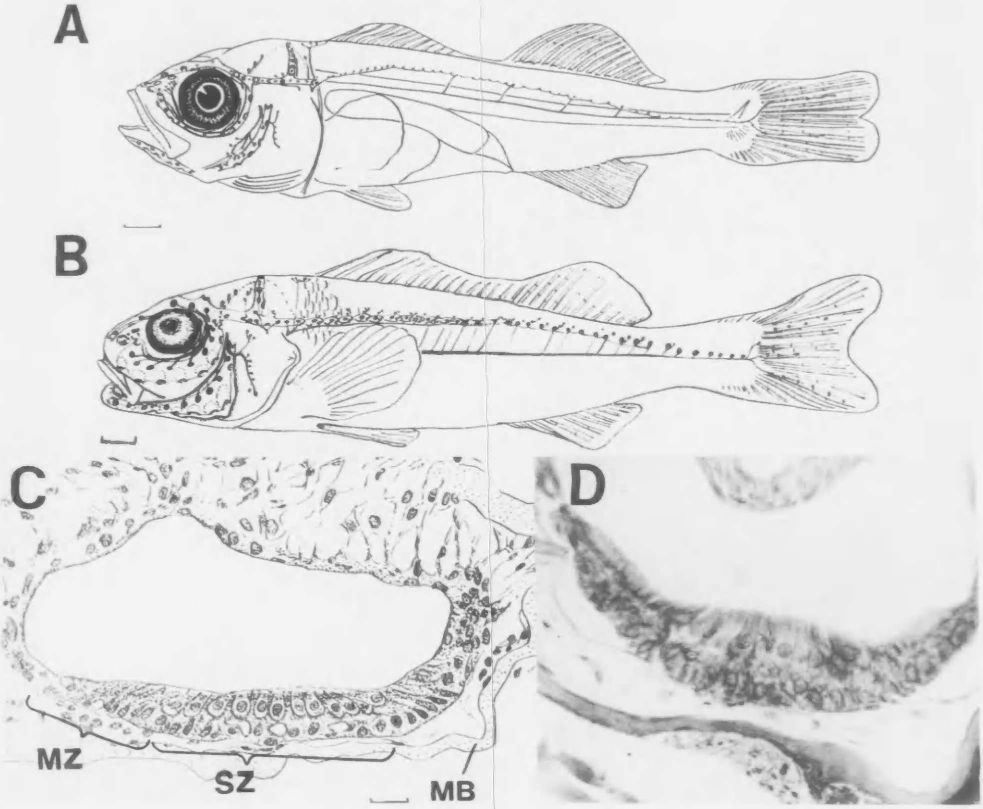

FIG. 5. Lateral line system in perch and ruff fry. A, Perch 22 days after hatching, 20 mm long; B, Ruff 37 days after hatching, 22 mm long; C, Neuromast of supraorbital canal, perch fry; D, Analogous neuromast, ruff larva. Scales and abbreviations as in Fig. 1.

ceca have developed and the second intestinal loop has formed (observations by N. O. Lange). In addition to the planktonic crustaceans eaten earlier the fry now begin feeding on small cyprinid larvae. The swimbladder takes up the entire upper part of the body cavity. The sense organs also change: the aperture of the olfactory fossa divides into two; most of the lateral-line canals on the head close, and their walls begin to ossify. Only small regions of infraorbital, temporal, supratemporal and opercular–mandibular canals remain open. The lateral-line canals of the body surface develop somewhat later. The size of the organs in canals increases (Fig. 5C). The number of the neuromasts in the lateral row increases up to 43 and two rows of sensory organs develop on the caudal fin. On the head, the number of secondary neuromasts increases. These remain open throughout life.

In the lake, perch fry 20–25 mm long school in midwater at a depth of 1.5 mm. The fish are very sensitive to vibrations in the water as well as to the motions of various underwater objects both of which stimulate them to sink to the bottom. As has been experimentally demonstrated, the object vision range increases to 5–6 cm, the school being kept together solely by visual orientation. At night the schools disperse and fry stay singly at the bottom. Perch fry 22–25 mm long can swallow cyprinid larvae (*Leucaspius delineatus*, *Carassius carassius*) 11–12 mm long; however, they school peacefully with similar-size fry such as those of roach (*Rutilis rutilus*).

In the last stage of the fry period, young gradually become similar to adults both in structure and in behavior. Lateral-line canal walls take the form of tubules and ossify gradually. The canal cavity connects with the external environments by apertures at the terminals of small canaliculi. These canaliculi branch off from the main canal between the adjoining neuromasts. On the head and trunk above the lateral canal, the development of new secondary (or accessory) neuromasts continues over a prolonged period after closure of the lateral-line canals. The fry respond to visual and acoustical stimuli in a differentiated manner, distinguishing them from background or normal stimuli, indicating perfection of the receptor contral chains. The main diet comprises planktonic and benthic organisms, with cyprinid fry (*L. delineatus, C. carrassius, Abramis brama*) accounting for an ever-increasing share.

In ruff, the fry stage begins at a length of 13.5–16.0 mm, 30–32 days after hatching. By that time, they differ rather considerably from perch fry (Fig. 5B). The head is flattened dorsoventrally. The eyes are relatively smaller than in perch, the lower vision field being somewhat delineated by the buccal surfaces. From the very onset the relative width of the canals formed in the head is greater in ruff than in perch. The canal neuromasts increase greatly in size (Fig. 5D). In addition, as the mantle zone proliferates the number of sensory cells there also increases and at the head and trunk surfaces some new secondary neuromasts or pit organs continue developing. It is noteworthy that on the trunk, they originate only above the lateral row of the primary neuromasts which are soon embedded in the canal. Development of scales proceeds concurrently with canal formation on the trunk. In fine structure, the sensory and supporting cells in the head neuromasts of ruff have attained the definitive state.

As with perch fry, secondary neuromasts continue to appear at the lateral surface of the trunk above the lateral canal and on the head, specifically in the buccal region and on the surface of the operculo-mandibular canal. Though the lateral canal in the scales remains rather narrow, it is broader than in perch. Head canals attain an unusually high state of development. In contrast to development in the perch their external walls fail to ossify fully, forming skin membranes stretched on thin bony bridges. Within the membranes, large neuromasts are found below these bridges. The canal is somewhat narrower at this site, the massive neuromasts cupula almost closing its lumen. On the membrane periphery, a small aperture remains between the adjoining organs leading from the exterior to the canal cavity (Fig. 5B).

In aquaria ruff fry keep near the bottom without forming schools. They are very sensitive to all kinds of stimuli, visual, tactile, and acoustical, and experiments have shown that they can feed on plankton organisms in the dark in contrast to such typical planktophages as *L. delineatus* fry, for which visual orientation is essential to feeding. They are very slow to adjust to background stimuli even those of such low intensity as footsteps in the room where the aquarium is kept. The response to sharp sounds or striking against the aquarium wall is so vigorous that the fry may jump out of the water. This sensitivity appears likely to account for the difficulty of keeping ruff fry in captivity, nervous shock causing their death in most cases. Under natural conditions, it manifests itself in the secretive mode of life of ruff fry, their twilight activity and their inhabiting rather deep parts of waterbodies.

Ultrastructural examination of neuromasts in ruff approaching adult age failed to reveal any major differences in the structure of sensory and supporting cells of these organs from those in the previously studied neuromasts of burbot (Flock 1965), pike (Aronova 1967), Japanese eel (Hama 1963, 1965; Yamada and Hama 1972), and gudgeon (Pomés-Delaveuve 1964a, b). However, in addition to the sensory and supporting cell types common to all of these neuromasts, the ruff has some special cells which we call "dark" cells (Smirnov 1975).

A sensory cell has a bundle of sensory hairs (Fig. 6A) at the apex comprising 15–20 stereocilia and one kinocilium. Scanning electron microscopic examination of ruff neuromasts opens to question the suggestion of kinocilium-independent motility (Vinnikov 1971). Although this cilium has an inner fibrillar apparatus of 9 peripheral paired fibrils and a pair of central filaments, it bends along with the stereocilia under the effect of external stimuli when buried in the cupula substance. The round nucleus with dispersed chromatin and 1–2 nucleoli is in the middle part of the sensory cell. The cytoplasm of the supranuclear region contains a larger number of irregularly shaped mitochondria, the Golgi complex, multivesicular bodies, cysternae of the endoplasmic reticulum as well as numerous microtubules associated with the substance of the "cuticular plate," a homogenous structure of medium electron density taking up the apical part of the cell. Short bundles of tonofibrils parallel to the cell membrane, and also polysomes, are likewise typical elements of this part of the cytoplasm (Fig. 6B). The round basal part of the cell is filled with various vesicles, among which lie mitochondria as well as cysternae of the endoplasmic reticulum. Agranular and granular nerve terminals forming the afferent and efferent innervation of these cells adjoin the basal parts of the sensory cells. At the sites of contacts with nerve terminals, structures of two types occur. Near the

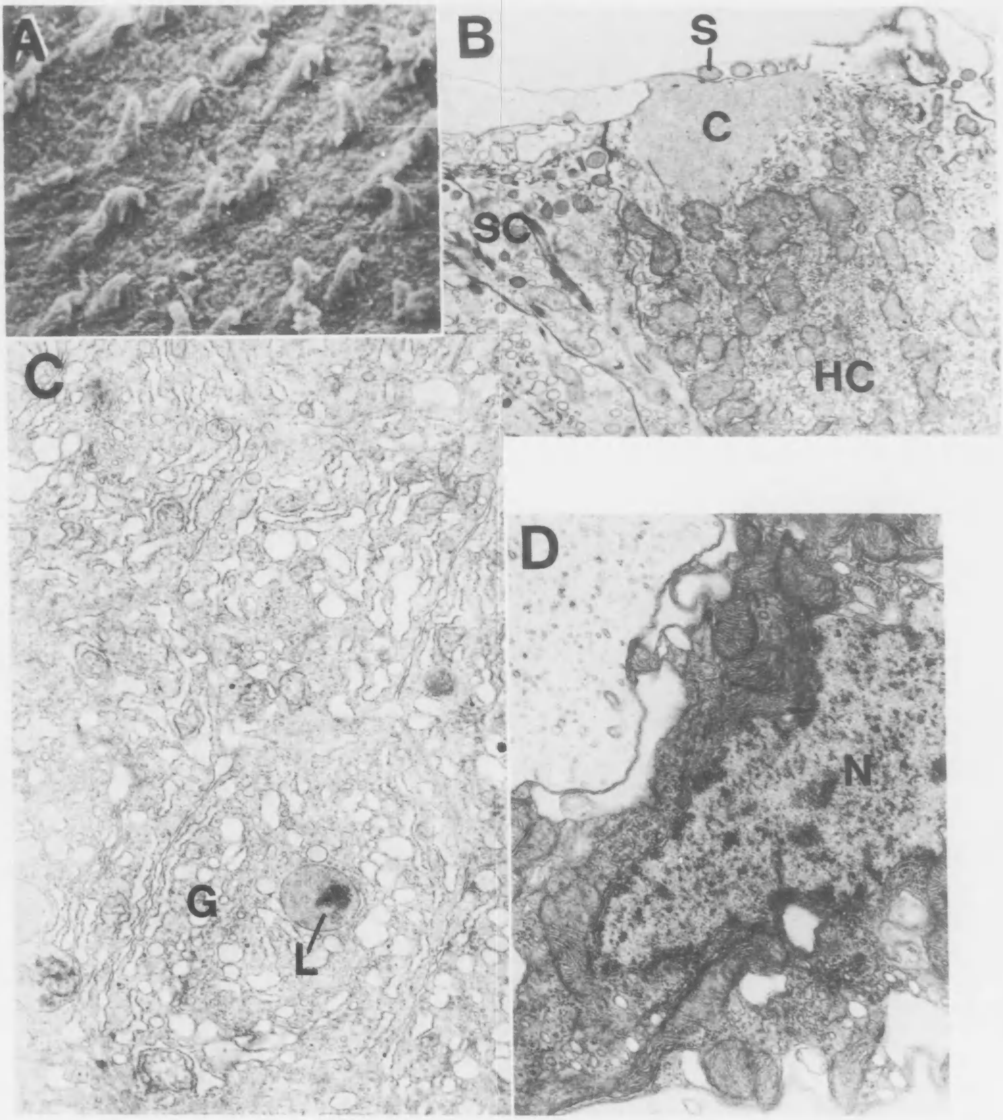

FIG. 6. Ultrastructure of neuromasts from the head canal of an adult ruff. A, Bundles of sensory hairs on sensory zone. Scanning micrograph, ×2000; B, Transverse section of a similar region, ×7200; C, Supranuclear region of a supporting cell with well developed Golgi complex, ×31,600; D, Fragment of a "dark cell," ×19,200. Abbreviations as in Fig. 2 except C — cuticular plate, L — lysome.

afferent terminals, there are osmiophilous presynaptic bodies varying in shape and surrounded by several rows of synaptic vesicles. In the efferent synaptic region, additional cysternae adjoining the cell membrane are found. Myelinated nerve fibers often occur in the neuromast epithelium. However, the myelin sheath disappears at a considerable distance from the nerve termination.

Supporting cell bodies are found between the basal membrane and receptor cell bases. Their lower parts are filled with membranes of granular endoplasmic reticulum (Fig. 6C), among which mitochondria and lysosomes occur. In the supranuclear zone, a well-developed Golgi complex is found; it has the appearance of numerous swollen dictiosomes varying in size. Narrow apical parts separating the sensory cells contain many round granules of various sizes and various electron densities. Elongated mitochondria and bundles of tonofibrils are found near the surface of the supporting cell (Fig. 6B).

"Dark cells" (Fig. 6D) occur singly within the neuromast sensory zones at the level of the lower part of the receptor cells. They are irregular in shape with a central nucleus, chromatin being distributed in lumps. Their cytoplasm is filled with a large number of mitochondria and various membranous structures. Sometimes it includes numerous large vacuoles with electron-opaque content. The function of these cells remains obscure.

Summary and Discussion

This ecomorphological study supports earlier sugestions that differences in the morphology and pattern of development of the lateral-line systems of young perch and ruff largely account for differences in their behavior at various stages although environmental conditions also play a role.

At hatching ruff embryos are less well developed than perch because of the lower oxygen content of the waters in which they develop. Accordingly the embryos are essentially sedentary and the onset of exogenous feeding is delayed and not very precise. In contrast free embryos of perch are very active and begin feeding exogenously as soon as the day after hatching, evidently a matter of necessity since a shortage of suitable food at that time can cause mass mortalities.

By the time their swimbladders are filled with gas larvae of both species are rather similar in structure and mode of life and a system of neuromasts has developed on the head from the anlagen connected with the embryonal placodes of the auditory region. Accordingly, they perceive large amplitude water vibrations and hence can detect the approach of predators. However, vision continues to play the leading role in the search for food.

Subsequently the behavior of perch and ruff diverges. Perch larvae turn to a schooling mode of life hunting plankton organisms in the upper layers of the offshore zone. Ruff larvae similar in structure remain singly near the bottom. The system of primary neuromasts develops extensively at the surface of the head and body of both species. Secondary organs start forming in association with the development of the multilayered epidermis. Perch larvae continue to orient largely by means of the organs of vision but in the ruff, as an adaptation to a benthopelagic mode of life, the lateral-line sensory organs become substantially more concentrated than those of the perch and begin to play a significant part in orientation and the search for food.

During the fry period the divergence increases. In both species the primary neuromasts on the head and trunk are embedded in canals. The head canals as well as the organs lying in them become increasingly different in the two species.

In the perch fry the secondary neuromasts do not appear to be highly sensitive, judging by the small number of sensory elements. The external walls of both the head and trunk canals become ossified, which coupled with the relatively small size of the organs in them, may protect the receptor structures from excessive stimulation during the extensive movements typical of the actively hunting young fish which begin to feed, in schools, on cyprinid fry and other relatively large prey. At night the perch fry rest on the bottom when the open organs above the trunk canal may serve to detect approaching danger.

In ruff fry the large neuromasts in the canals, with continually increasing numbers of sensory cells, presumably add to the sensitivity of the system and allow detection of very weak vibrations in the water. Moreover, the complex structure of the membranes, oriented in different directions in the external walls of the head canals appear also to augment sensitivity and to help to localize the source of vibration which is presumably important to a solitary, secretive fish which feeds on or near the bottom in low light conditions on midge larvae, other bottom fauna and the larger planktonic forms. The pit organs found in large numbers above the lateral line and on the upper and lower surfaces of the head may serve to detect the much stronger vibrations caused by the movement of large predators in the water. Certainly ruff fry are very sensitive to such vibrations being very difficult to accustom to the noises occurring in the laboratory.

The perch displays greater ecological plasticity than the ruff. Observations in small natural ponds and in Glubokoe Lake have shown that not all perch fry adopt the schooling habit. Some lead solitary lives as ambush predators having a home range. In many waters slow-growing inshore perch feeding on benthic organisms coexist with fast-growing predatory pelagic perch (Toltshanov 1952; Dianov 1955; Tesch 1957; Popova 1965). Heterogeneity in growth rate among young perch can be detected as early as the larval stage. To date, a comparative study of the sensory organs of the two forms has not been undertaken. However, there is reason to believe that morphological differences may be insignificant. Hence, perch can use the receptor capabilities of the lateral line system quite differently depending on the given conditions.

Acknowledgments

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Morphology, Physiology, Behavior, and Ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill[1]

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THORPE, J. E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. J. Fish. Res. Board Can. 34: 1504–1514.

A review of literature on *Perca fluviatilis* and *P. flavescens* indicated one difference (in the position of the predorsal bone) sufficient to maintain their separateness as species. Otherwise they are overwhelmingly equivalent biologically. Their distributions are limited by the same effects of temperature, current speed, salinity, and dissolved oxygen. They are similar in gonadal development and age at first maturity; in the effects of water temperature and latitude on spawning time, and of environmental fertility on fecundity; in spawning behavior, fecundity, and the course of larval development. Growth capacities are similar and their expression subject to population density and temperature in the same way. Both species are adapted to a diet of small live animals, but will take whatever is available; cannibalism is characteristic, and may begin at the same early feeding stage. The two species show similarities in diurnal periodicity of feeding and in total food consumption. They also have the same pattern of development of light responses, of schooling, of activity and of daily and seasonal migrations. Within the fish community they fulfill the same role as converters of invertebrate foods into a form suitable for consumption by terminal fish predators, especially *Stizostedion* spp., influencing the population dynamics of their predators in similar ways.

Key words: Percidae, morphology, physiology, ecology, *Perca*, life history, growth, reproduction, yellow perch, Eurasian perch

THORPE, J. E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. J. Fish. Res. Board Can. 34: 1504–1514.

Une revue de la littérature portant sur *Perca fluviatilis* et *P. flavescens* indique une différence (dans la position de l'os prédorsal) suffisante pour maintenir leur rang d'espèces distinctes. Par ailleurs, elles sont biologiquement très semblables. Les mêmes facteurs, température, vitesse des courants, salinité et oxygène dissous limitent leur distribution. Elles se ressemblent quant au développement des gonades et à l'âge de la première maturité; quant aux effets de la température de l'eau et de la latitude sur la période de fraie, et de la fertilité ambiante sur la fécondité; quant au comportement de fraie, à la fécondité et à l'évolution du développement larvaire. Les potentiels de croissance sont semblables, et la densité de population et la température affectent la croissance de la même façon. Les deux espèces sont adaptées à un régime alimentaire de petits animaux vivants, mais elles avaleront ce qui est disponible; le canibalisme est caractéristique et peut commencer au même stade du début de l'alimentation. Les deux espèces démontrent des similitudes dans la périodicité nycthémérale d'alimentation et dans la consommation totale de nourriture. Elles ont également des schémas identiques de développement des réponses à la lumière, de formation de bancs, d'activité et de migrations journalières et saisonnières. Dans la communauté de poissons, elles jouent le même rôle de convertisseurs d'invertébrés en une nourriture convenable pour les poissons prédateurs finals, surtout *Stizostedion* spp., influençant la dynamique des populations de leurs prédateurs de façons identiques.

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THE Eurasian perch, *Perca fluviatilis* L., is widely distributed from sea level to just over 1000 m altitude in Eurasia, and has been introduced into Australia, New Zealand, and South Africa (Thorpe 1977b, fig. 4). The yellow perch, *P. flavescens* Mitchill, occurs over the same altitudinal range, but solely in North America (Thorpe 1977b, fig. 4). Despite their geographical isolation, this paper shows that these fish are so similar in morphology, physiology, behavior, and ecology that they should be considered

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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TABLE 1. Relative lengths of spiny fin rays and cranial characteristics of *Perca fluviatilis* and *P. flavescens* (adapted from Svetovidov and Dorofeeva (1963) except for data from Georgian Bay, Lake Huron, which is original).

Characteristic	Locality	*P. fluviatilis*	*P. flavescens*
1st dorsal spine			
as % of 1st anal	European USSR	86.1–133.3	—
	Yenisei River	74.6–148.6	—
	Lena River	56.1–129.5	—
	Kolyma River	33.0–121.5	—
	North America	—	36.3–83.2
	Georgian Bay	—	37.1–73.0
as % of 2nd dorsal	European USSR	70.0–93.9	—
	Yenisei River	63.4–92.2	—
	Lena River	55.2–90.0	—
	Kolyma River	36.9–84.0	—
	North America	—	34.8–69.0
	Georgian Bay	—	39.4–64.5
Width of cranium as			
% of length of its base lateral ethmoid	Eurasia	33.1–35.7	—
	North America	—	29.3–32.9
frontal	Eurasia	32.6–37.3	—
	North America	—	27.5–32.1
sphenotic	Eurasia	46.1–52.2	—
	North America	—	44.9–46.1
pterotic	Eurasia	49.4–53.3	—
	North America	—	47.3–50.0
Interocular interval	European USSR	21.4–26.1	—
as % of head length	Kolyma River	20.6–29.0	—
	North America	—	17.9–24.6

biologically equivalent. Although some authorities (e.g. Banarescu 1960; Bailey et al. 1970) consider the taxa as separate species, others (e.g. Svetovidov and Dorofeeva 1963; McPhail and Lindsey 1970) treat *P. flavescens* as a subspecies of *P. fluviatilis*. Fuller treatment of the evidence cited in this paper is to be found in a synopsis of biological data on the perches (Thorpe 1977b).

Morphology

Pokrovskii (1951) showed that several length relationships between spiny fin rays of the two perches were independent of fish size (unlike relative lengths of gill filaments used by Berg (1905), which changed with growth), and Svetovidov and Dorofeeva (1963) used such ratios to compare fish from Europe, Siberia, and North America (Table 1). They also compared the opercular bones, positioning of pectoral fins, width of the cranium, and shape of the supraoccipital crest, and in all these characteristics found a directional trend in their ranges of variation from west to east, that is from Europe through Siberia to North America. More distinct cranial and skeletal differences exist between *P. schrenki*, the Balkhash perch, and *P. fluviatilis* than between the latter and *P. flavescens* (Zhadin 1949) even though all three forms are considered to have had a common ancestor, and *P. fluviatilis* and *P. schrenki* have contiguous distributions. However, Collette and Bănărescu (1977) have shown that the predorsal bone in *P. flavescens* is inserted between the first and second neural spines, whereas in *P. fluviatilis*, it occurs anterior to the first neural spine. As *P. fluviatilis* agrees in this structure with *P. schrenki* and with *Gymnocephalus* spp., the character is interpreted as an adequate criterion of specific status for *P. flavescens*. In number of fin rays, scales, vertebrae, size of eggs, and larvae (Table 2), *P. flavescens* falls within the range of variation of *P. fluviatilis*.

Physiology

Tolerances — The distributions of the two perches reflect their physiological tolerances of temperature, current speed, salinity, and dissolved oxygen concentration. Weatherley (1963a, b) concluded from his experiments on *P. fluviatilis* and those of Hart (1952) on *P. flavescens* that neither species could survive for more than a few hours at 31 °C; the lower latitudinal limit of known distributions of perch in Italy, Australia and the U.S.A. corresponded closely with the 31 °C summer isotherm.

TABLE 2. Comparison of morphological characteristics of *P. fluviatilis* and *P. flavescens*.

Character	*P. fluviatilis*	*P. flavescens*
Fin rays:		
1st dorsal	12–17 (Suskiewicz 1961)	13–15 (Scott and Crossman 1973)
2nd dorsal	1–3/12–16 (Serov 1959; Spillman 1961)	1–3/12–15 (Scott and Crossman 1973; McPhail and Lindsey 1970)
pectoral	12–17 (Thorpe (unpubl.); Berg 1949)	13–15 (McPhail and Lindsey 1970)
ventral	1/4–6 (Suskiewicz 1961; Spillman 1961)	1/4–5 (McPhail and Lindsey 1970)
anal	2/7–10 (Berg 1949)	2/6–9 (Scott and Crossman 1973; Driver and Garside 1966)
Scales:		
lateral line:	53–77 (Spillman 1961; Berg 1949)	51–70 (Scott and Crossman 1973; Day 1880–4)
rows above	7–10 (Berg 1949)	6–9 (Day 1880–4; Thorpe, unpublished data)
rows below	12–22 (Berg 1949; Spillman 1961)	13–18 (Thorpe, unpublished data; Day 1880–4)
Vertebrae:	38–43 (Collette 1963)	38–42 (Scott and Crossman 1973; Collette 1963)
Eggs:		
diameter (mm)	1.0–1.9 (Pihu 1964; Lake 1967)	1.0–2.1 (Schneider, personal communication; Mansueti 1964)
diameter after hardening (mm)	1.9–2.4 (Lake 1967)	1.9–2.8 (Mansueti 1964)
maximum diameter (mm)	5.1 (Lake 1967)	4.5 (Mansueti 1964)
yolk diameter (mm)	1.1–1.4 (Lake 1967)	1.0–1.6 (Schneider personal communication; Mansueti 1964)
Oil globule diameter (mm)	0.4–0.8 (Lake 1967; Laskar 1943)	0.4–0.9 (Schneider, personal communication; Mansueti 1964)
Larva:		
length at hatching (mm)	4.8–6.0 (Lake 1967; Laskar 1943)	4.1–6.6 (Mansueti 1964)

Kreitmann's (1932) value for sustained swimming speed for *P. fluviatilis* as 2–3 body lengths per second corresponds closely with that of approximately 2.2 body lengths per second, which can be derived from the data of Bardach (1951) and Hergenrader and Hasler (1967) for *P. flavescens*. Weatherley (1963b) concluded that mountain ranges prevented the natural extension westward in America and southward in Europe since the fish were unable to withstand the high stream velocities.

Privolnev (1970) showed that *P. fluviatilis* could live normally at 10‰ salinity during a 3-wk experiment, but did not tolerate higher concentrations. The Eurasian perch is found in brackish water of the Baltic Sea at 7–10‰ (Tesch 1955; Neuman 1974), the Aral Sea at 10‰ (Letichevskii 1946), but not the Caspian Sea at 12‰ (Berg 1965). Yellow perch have been reported in Chesapeake Bay at 13‰ (Hildebrand and Schroeder 1928) but mainly at 5–7‰ (Muncy 1962) and in Manitoba lakes at 0.3–10.3‰ (Driver and Garside 1966).

Jones (1964) gave limiting concentrations of dissolved oxygen for survival of Eurasian perch as 1.1–1.3 ppm at 16°C, and of yellow perch as 0.4–0.9 ppm at 15.5°C and 2.25 ppm at 20–25°C. These levels, which correspond closely for the two species, are expressions of capacity rather than preference. As Jones points out, a more meaningful measure is that of the critical level below which activity (in the broadest sense of all metabolic processes additional to the resting minimum) is restricted. Fry (1957) determined this level as 7 ppm oxygen at 20°C for yellow perch; Wunder (1936) gave 7–10 ppm for Eurasian perch. The critical level for survival of caged Eurasian perch in a Swedish lake was 7 ppm (Andreasson and Ståke 1970), and signs of respiratory distress were found at this level among Lake Erie O+ yellow perch by Petit (1973).

Reproduction — Gonad development, age at first maturity, fecundity, time of spawning, spawn, incubation time, and larval development correspond closely for the two perches.

Turner's (1919) description of development of the testes of *P. flavescens* is paralleled almost exactly by Le Cren's (1951) for *P. fluviatilis*. The development of the ovaries in yellow perch (Lagler et al. 1962) also appears to be identical to that in Eurasian perch (Le Cren 1951). Male Eurasian perch usually mature during their second year of life and the females 1–2 yr later (Tesch 1955). In some fast-growing populations the males may mature during their first year (Petrovski 1960), and in slower-growing stocks not until their third year (Ereshchenko 1959). Male yellow perch also usually mature in their second year and females in their third (Hile and Jobes 1941; Hasler 1945; Herman et al. 1964), but Scott and Crossman (1973) regard third and fourth years, respectively, as more common.

Fecundity varies widely between populations of the two perches. It also varies within populations, as for example in the Volga Delta stock (Popova 1965) and in Lake Baikal (Evtyukhova-Rekstin 1962). The within-habitat studies suggest that some of the variation is attributable to differences in food-supply, in conditions for spawning, and in degree of exposure to wind. Environmental fertility was held by Petrovski (1960) to account for the high fecundity of Dojran Lake perch, Yugoslavia, and by Tsai and Gibson (1971) for that of Chesapeake Bay perch as compared with those from Lake Ontario (Sheri and Power 1969). All measures of fecundity of yellow perch (range 3,035–109,000) fall within the range recorded for Eurasian perch (950–210,000).

Both perches spawn in the spring in shallow water, where the single, convoluted egg-strand is attached to submerged plants or fallen trees (e.g. Echo 1955; Holčik 1969). Spawning has been reported for both species as at night (Kammerer 1907; Lake 1967; Eddy and Surber 1960; Breder and Rosen 1966) and by day (Chevey 1925; Hergenrader 1969). It has been suggested for both fishes that either photoperiod or temperature is the proximate determinant of the onset of spawning, but no critical experimental test of these hypotheses has been published. Available evidence on temperature at and date of the start of spawning (Table 3) is equivocal. Whereas for example Nikitinsky (1928), Berzins (1949), Popova (1965), and Chikhova (1973) all imply that temperature controls the onset of spawning in *P. fluviatilis*, and Amundrud et al. (1974) likewise in *P. flavescens*, Hergenrader (1969) observed aquarium yellow perch spawning at 14°C on the same day as wild fish spawned at 8°C in Lake Mendota just outside the aquarium. In general, spawning starts at a lower temperature and at a later date as latitude increases (Fig. 1). The scatter of values decreases with increasing latitude, so that the greater dispersion of *P. flavescens* data is probably a function of their southerly origin. On evolutionary grounds it is likely that spawning time would be determined by the subsequent availability of adequate food resources for the fry. In the lower-latitude localities the increased complexity of the fish communities and of their forage resources as compared with the less diverse high-latitude communities should lead to a broader range of local specialization, of which the scatter of points in Fig. 1 is an expression.

The highly distinctive egg-strand of perch, forming a hollow, twisted cylinder up to 2 m in length, was described for *P. flavescens* by Worth (1892). His account does not differ from that of Chevey (1925) for *P. fluviatilis*.

Swift (1965) and Kokurewicz (1969), using *P. fluviatilis*, and Hokanson and Kleiner (1975), using *P. flavescens*, have found the same relationship between incubation time and temperature.

Mansueti (1964), describing the development of yellow perch eggs and larvae from Chesapeake Bay material, noted that the whole series of descriptions and illustrations of larval and juvenile development of *P. fluviatilis* given by Konstantinov (1957) corresponded precisely with hers, not only in appearance but also in timing of fin-formation at specific larval size and in the sequence of formation of internal organs. Scale formation begins at a total length of 2.0–2.5 cm in Eurasian perch (Segerstråle 1933) and at 2.4 cm in yellow perch (Pycha and Smith 1955).

Growth — Tesch (1955) reviewed growth studies of both perches, and grouped growth-rate into five categories concerning age and total length:

Category	Age-group	Length (cm)
Very good	II	>20
Good	III	>20
Moderate	III	>16
Poor	III	<16
Very poor	All fish	<16

He proposed a standard corresponding to his moderate growth-rate category, which compares closely with data on yellow perch (Carlander 1950) at least to age V (Table 4). Examples from Europe and North America show that the growth capacities of the two perches are similar, and that their expressions are subject to the same environmental controls, e.g. inverse density-dependence (Eschmeyer 1937, 1938; Alm 1946; Beckman 1950; Tesch 1955) and summer water temperatures (Le Cren 1958; Coble 1966). Tesch further suggested that optimal conditions for perch were in large, not too shallow, weed-free

TABLE 3. Spawning periods of *P. fluviatilis* and *P. flavescens* in various localities with latitudes (°N except as indicated), and water temperatures (°C) at beginnings of periods.

Locality	Latitude	Spawning period	Water temperature	Authority
		P. fluviatilis		
Lake Dojran	41	March		Petrovski (1960)
Kuban Delta	45	Mar. 15–early Apr.		Berg (1965)
Lago Maggiore	46	Apr. 15–May 15	9	Grimaldi[a]
Kuchurgan Liman	47	Mar. 10–Apr. 9		Berg (1965)
Bodensee	47	Apr.–May		Hartmann (1975)
North Kazakhstan lakes	46–51	Apr. 20–May 20	11	Ereshchenko (1959) Shilenkova (1959)
Volga Delta	48–49	May–early June	8	Popova (1965)
Upper River Vistula	50	end Apr.	8	Suskiewicz (1961)
Kličava Reservoir	50	Apr. 23–May 3	8	Stehlik (1968)
Slapton Ley	50	Apr. 13–early May	8.5	Craig (1974)
Rostherne Mere	53	end Apr.–May		Banks (1970)
Kuybyshev Reservoir near dam	53	May 12–24	8.5	Chikhova (1973)
Lough Corrib	53½	Apr. 19 onwards	10.6	Kennedy[b]
Lough Mask	53½	Apr. 23 onwards	12	Kennedy[b]
Lough Sheelin	54	early Apr. onwards		Kennedy[b]
Lough Arrow	54	Apr. 22 onwards	9.4	Kennedy[b]
Windermere	54	May 2–early June	8.8–11.8	Le Cren (1951, 1958); Craig[a]
Grosser Plöner See	54	end Apr.–May	< 14	Laskar (1943)
Kuybyshev Reservoir, bays	54	May 1–5	8.5	Chikhova (1973)
Lake Chany	55	May 15–31	11	Tyurin (1935)
River Atmata	55	end Apr.–May	< 14	Vashkyavichyute (1963)
Lake Zarizino	56	May 2–13	8.2	Nikitinsky (1928)
Yakhromsk Reservoir	56	Apr. 23–early May	6	Konovalova (1955)
Loch Leven	56	Apr. 21–May	9	Original data
Yenisei River, Krasnoyarsk	56	mid-May–early June		Krasikova (1958)
Lake Ilmen	58	Apr. 20–5 May	7	Evropeitseva (1949)
Rybinsk Reservoir	58–59	Apr. 15–13 May		Zakharova (1965) and Svetovidova (1960)
Hjälmaren/Mälaren	59	mid May–mid June		Rundberg (1977)
Baltic Sea, Askö	59	May 29–early June	8.5	Aneer and Grahn[a]
River Ob, Narym	59	May 6–31	5.8	Bashmakov, in Dryagin (1948)
Yenisei River, Near Yartsevo	60		8	Dulkeit, in Krasikova (1958)
Neva Bay, Baltic	60	Apr. 30–May	7	Grib (1949)
Lake Mjösa	61	end May		Huitfeld-Kaas (1916)
Karelian lakes	62	early May	7	Zhakov (1964)
River Ob, Kondinskoe	63	May 27–June 17	7	Dryagin (1948)
Lake Munduyisk	68	mid June–early July		Krasikova (1958)
Hildenlampi	69	May 24–June 14	5	Kukko et al. (1972)
Kolyma River	69	end June–July		Berg (1965)
Yenisei River, Dudinka	69½	end June–July		Krasikova (1958)
New South Wales, Australia	30–36°S	Aug. 1–15	11.5	Lake (1959, 1967)
Victoria, Australia	34–38°S	October		Tunbridge (1972)
Whole range	41–69½	March–July	5.0–11.8	
		P. flavescens		
Potomac River	38	Feb–Apr.	8.3	Leach (1928)
Patuxent River	38	Mar. 20–25	8.5	Tsai and Gibson (1971)
Severn River	39	March	5.6	Muncy (1962)
Klamath River	42	Mar. 28–May 18	8.0	Coots (1956)
Lake Mendota	43	April	8.0	Hergenrader (1969)
Oneida Lake	43	Apr. 15–30		Forney (1971)
Lake Francis Case–Lake Oahe	43–47	early Apr.–May	8	Nelson and Walburg (1977)
Lake Ontario, Bay of Quinte	44	May–June		Sheri and Power (1969)
Lake Ontario, Collins Bay	44	end Apr.–May	c. 10	Keast (1968)
Lake Huron	44	Apr. 15–May		El-Zarka (1959)

TABLE 3. (*Concluded*)

Locality	Latitude	Spawning period	Water temperature	Authority
Lake Michigan	42–47	Apr.–May	7.2	Herman et al. (1964)
Lake Opinicon	44½	end Apr.–May	<9	Amundrud et al. (1974)
Lakes Tamaracouta and Archambault	46	mid-May–mid-June		Newsome and Leduc (1975)
Central Minnesota lakes	46	Apr.–early May	7	Eddy and Surber (1960)
Round Lake, Idaho	47	May	c.7	Marcuson and Howse (1968)
Red Lakes	48	mid-Apr.–May		Pycha and Smith (1955)
Thompson Lake	48	May 5–17	14	Echo (1955)
Okanagan Basin	50	Apr.–May		McPhail and Lindsey (1970)
Qu'Appelle Lakes	50	May	10	Atton[a]
West Blue Lake, Manitoba	51	probably early June		Ward[a]
Ile de la Crosse	55½	end May–June	9	Atton[a]
Whole range	38–55½	Feb.–June	5.6–14	

[a]Personal communication.
[b]Unpublished data.

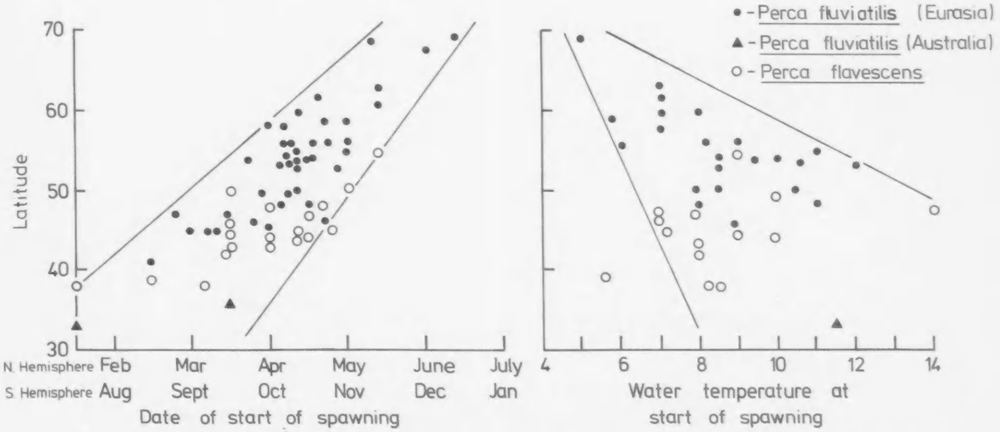

FIG. 1. Dates of, and water temperature (°C) at, beginning of spawning of *P. fluviatilis* and *P. flavescens* in relation to latitude (°N except as indicated). Data from many authors, acknowledged in the text.

mesotrophic waters containing a substantial population of forage fish such as roach (*Rutilus rutilus*) or smelt (*Osmerus eperlanus*). Such conditions allow moderate growth and a high yield among *P. fluviatilis* stocks; similar conditions occur in the Laurentian Great Lakes, where *P. flavescens* shows moderate to good growth (Hile and Jobes 1942) and high yield (Baldwin and Saalfeld 1962). Frank (1967) showed that there was no substantial difference in average growth of O+ perch from the two sides of the Atlantic. Thus the growth patterns under similar ranges of environmental conditions are similar for Eurasian and yellow perch.

Behavior and Ecology

Spawning — The details of the spawning act differ little between the two species as recorded by Kammerer (1907), Fabricius (1956), Fabricius and Gustafson (1959), Harrington (1947), and Hergenrader (1969). In Europe Nikitinsky (1928) and in America Tsai and Gibson (1971) found that the males preceded the females on to the spawning grounds, where egg-laying lasted only 2–3 days. In brackish water populations both species usually move into freshwater to spawn (Henking 1923; Muncy 1962; Neuman 1974) although Nikolskii (1940) reported that

TABLE 4. Total lengths (cm) of *P. fluviatilis* (Tesch's (1955) standard) and *P. flavescens* (Carlander 1950) at various ages.

Age	*P. fluviatilis*	*P. flavescens*
O	8.0	1.8–10.4
I	12.2	5.0–18.5
II	14.8	6.6–25.9
III	18.9	8.3–28.1
IV	21.8	10.4–31.5
V	25.2	12.3–31.5
VI	31.4	15.2–34.8
VII	36.8	17.8–34.0
VIII	39.5	18.8–33.0
IX		21.6–34.3
X		26.4–32.5
XI		32.1
XII		30.7
Maximum length (cm)	62.0[a]	53.0[b]
Maximum weight (kg)	10.4[c]	1.9[d]

[a] Leopold (personal communication).
[b] McPhail and Lindsey (1970).
[c] Lake (1959).
[d] Scott and Crossman (1973).

P. fluviatilis spawned both in the Aral Sea and in its inflowing waters.

Food and feeding — The diets of both species progress from rotifers (Teodorescu 1943; Siefert 1972) to Entomostraca (Rogowski and Tesch 1960; Pycha and Smith 1955) and thence to benthic insect larvae, crustaceans, molluscs, and leeches, rapid growth being assured if fish and crayfish (*Astacus* spp.) are available (e.g. Shilenkova 1959; Schneider 1909; Clady 1974; Ward and Robinson 1974). Herman et al. (1964) stated that the yellow perch is adapted to a diet of small live animals and will take whatever is available; in this it behaves exactly as its Eurasian relative. Cannibalism is universal in perch, beginning at the fry stage (Smyly 1952; Clemens et al. 1924; Ilina 1973) with fish of only 2.1–2.5 cm. Diurnal periodicity of feeding has been demonstrated in both species (Manteifel et al. 1965; Keast and Welsh 1968; Fortin and Magnin 1972b; Thorpe 1974, 1977a) but the details of the feeding rhythm differ slightly between localities (rather than between species), probably in response to food availability. Total food consumption varies seasonally in the two perches in the same way, being maximal at midsummer and declining to maintenance levels in early autumn (Schneider 1973; Thorpe 1974, 1977a).

Light reactions — Laboratory (Chevey 1925; Privolnev 1956) and field (Scheuring 1930; Ridenhour 1960) studies indicate that fry of both species aggregate in bright diffuse light until about 2 mo after hatching. At this time they select darker areas, cease to be pelagic, and become demersal.

Schooling, activity and movements — During the day both species form schools, stratified by size and age (Hasler and Bardach 1949; Kukko and Lind 1972), and these schools disperse at evening twilight to reform at morning twilight (Hasler and Villemonte 1953; Hergenrader and Hasler 1966; Alabaster and Robertson 1961; Siegmund and Wolff 1973). Eriksson (1974) found that *P. fluviatilis* was active diurnally at all seasons, but its level of activity, like that of *P. flavescens* (Hergenrader and Hasler 1967), increased with increasing temperature. Regular daily movement from a nocturnal resting area to a diurnal active area has been observed for both perches (Scott 1955; Ohlmer and Schwartzkopff 1959). Seasonal migration from deepwater wintering areas to shallow-water spawning areas in the spring is characteristic of both species (Forney 1971; Thorpe 1974). Within-lake movement is often restricted (Fortin and Magnin (1972a) found average distances travelled by marked fish to range from 1.9 to 3.9 km in Lac Saint-Louis, Quebec) and may lead to the formation of discrete local populations (Chikhova 1973). However, wanderings of 50–57 miles have been recorded for Eurasian perch in the Baltic (Henking 1923) and yellow perch in Lake Michigan (Smith and Van Oosten 1939), respectively.

Position in the community — Both species of perch function as important converters of invertebrate foods into a form suitable for ingestion by terminal fish predators. In America the chain consists typically of *Daphnia* spp. — *P. flavescens* — *Stizostedion vitreum vitreum* (Ward and Robinson 1974); in Europe it is *Daphnia* spp. — *P. fluviatilis* — *Stizostedion lucioperca* (Vasilev 1955). The terminal position may also be occupied by *Esox lucius* (Lawler 1965; Thorpe 1974) or by *Lota lota* (Zadulskaya 1960; Lawler 1963). Parallel fluctuations of perch and their predator populations have been recorded in both continents (Smith and Krefting 1954; Alm 1957) and Forney (1974) showed that the abundance of young perch governed the intensity of predation of *Stizostedion* sp. on other fish, indirectly controlling the *Stizostedion* population by regulating cannibalism.

Conclusion

The difference between the perches in the position of the predorsal bone appears to be an evolutionary change consequent on temporal separation since Pleistocene times. It does not appear to be important biologically, and in view of their overwhelming similarities in all other characteristics it seems prudent to regard the two fishes as functionally the same.

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Morphological, Physiological, and Ethological Differences Between Walleye (*Stizostedion vitreum vitreum*) and Pikeperch (*S. lucioperca*)[1,2]

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MARSHALL, T. R. 1977. Morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). J. Fish. Res. Board Can. 34: 1515–1523.

A review of the literature indicated that pikeperch (*Stizostedion lucioperca*) are generally more tolerant than walleye (*S. vitreum vitreum*) of a wide range of environmental sources of stress, such as organic pollution, sedimentation, and fluctuating water levels. This advantage presumably arose from numerous morphological and physiological specializations which are expressed through appropriate behavioral patterns. Of prime importance is the ritualistic redd building and guarding behavior developed by the pikeperch which contributes to a consistently successful rate of fertilization and lowered mortality of their eggs and larvae. In addition, pikeperch have a much higher fecundity and require a less specific set of spawning conditions than do walleye. These attributes allow the pikeperch much greater reproductive success under stressful conditions and thus more flexibility in their range.

Key words: behavior, cultural eutrophication, environmental stress, morphology, physiology, pikeperch, reproductive potential, reservoirs, *Stizostedion*, walleye

MARSHALL, T. R. 1977. Morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). J. Fish. Res. Board Can. 34: 1515–1523.

Une revue de la littérature indique que le sandre (*Stizostedion lucioperca*) est généralement plus tolérant que le doré jaune (*S. vitreum vitreum*) à une gamme étendue de sources ambiantes de stress, telles que la pollution organique, la sédimentation et les fluctuations du niveau de l'eau. Cet avantage résulte probablement de nombreuses spécialisations morphologiques et physiologiques qui s'expriment par des modalités appropriées de comportement. La construction rituelle de sillons de fraie et le comportement de garde développés par le sandre ont une importance capitale: ils contribuent à assurer un taux de fécondation uniformément élevé et une diminution de la mortalité des œufs et des larves. En outre, le sandre est beaucoup plus fécond et a besoin d'un ensemble de conditions de fraie beaucoup moins spécifiques que le doré jaune. Grâce à ces attributs, le sandre a un succès de reproduction beaucoup plus grand dans des conditions difficiles et, partant, plus de flexibilité dans sa distribution géographique.

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A review of the literature was undertaken to establish the major morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). This paper describes some of these characteristics and attempts to relate them to the present day distribution and success of the taxa. Special emphasis is given those attributes which have proven instrumental in the pikeperch's survival in culturally advanced trophic systems and reservoirs.

It has been proposed that all contemporary members of the genus *Stizostedion* originated in Eurasia, where the ancestors of the three North American species radiated via a land bridge or archipelago across the North Atlantic, between the Oligocene and Pleistocene periods (Svetovidov and Dorofeeva 1963). Accordingly, walleye and pikeperch have evolved over the past several million years as spatially discrete taxa.

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Humid continental and west-coast marine climates (moderated by the Gulf Stream) prevail over most of the pikeperch's range in Europe and contribute to a generally warmer and seasonally less variable climate than that found at equivalent latitudes of North America. There, much of the walleye range is influenced by a high-latitude continental climate (Bradley 1950), with seasonal extremes in temperature. In addition, lakes and rivers of Europe have been subjected to large organic inputs from a denser human population and over a much longer period of time than in comparable situations in North America, resulting in the cultural eutrophication of many European water systems. Pikeperch possess a number of unique characteristics which enable them to flourish in these advanced trophic conditions, which would probably inhibit walleye reproduction or perhaps even prove lethal.

Morphology

Pikeperch and walleye have nearly identical meristic counts (Table 1) and are superficially similar in appearance due to the commonality of a number of generic traits. Close examination, however, reveals many small structural differences. Pikeperch are slightly terete in cross-section with a proportionately smaller, more streamlined head and a deeper, more robust caudal peduncle than the walleye (R. A. Ryder unpublished data). The maximum body depth in relation to body length is consistently greater for the pikeperch, as is the ratio of the base of the pelvic fin to the interpelvic width (Shcherbukha 1968; Scott and Crossman 1973). In this way the pikeperch appears morphologically closer than does the walleye to the genus prototype which resembles the contemporary genus *Perca*.

Though both species have a subretinal tapetum lucidum consisting of a light-reflecting pigment, its effective area is relatively smaller in the pikeperch (Wunder 1930; Moore 1944; Ali and Anctil 1968). In addition, the ratio of eye diameter to head length is much smaller for the pikeperch than for the walleye (Shcherbukha 1968; Scott and Crossman 1973).

The gill rakers of the two species are unique. In walleye, the inner edge of the gill arch supports a series of stublike "knobs" adorned with short, tooth-bearing processes. Similar processes extend laterally on a series of elongated rakers supported by the outer edge of the arch. Approximately the same number of rakers are present in pikeperch, but they are all of one variety, that is, stubby, tooth-bearing nodules similar to those found along the inner gill arch of walleye.

Slight to substantial color differences exist between the two species, and subpopulations of each vary with the turbidity of the water that they inhabit. The back and sides of pikeperch (Schindler 1957) are greenish to blue-grey, with the underside silvery white or bluish. The dorsal fins have longitudinal rows of black spots, whereas the caudal fin is spotted in transverse rows. Other fins are yellowish grey. Background colors of the walleye (Scott and Crossman 1973) range from olive-brown through golden brown to yellow, with the dorsal surface somewhat darker than the sides and the ventral surface milk-white or yellow-white. The second dorsal and caudal fins have regular rows of tiny spots, whereas the first dorsal fin is unmarked except for a black blotch present at its posterior-basal border. The lower tip of the caudal and tip of the anal fin are milk-white.

Color can be used to distinguish the sexes in pikeperch, the male often exhibiting a dark pigment on its ventral surface whereas the female is lightly colored or immaculate. The genital papilla, which protrudes in the female, is another distinguishing characteristic (Gaschott 1928). Superficial sexual dimorphism is not apparent in the walleye.

The pikeperch has four to six pyloric caeca, whereas three are usually present in the walleye (Gaschott 1928; Scott and Crossman 1973). R. A. Ryder (unpublished data) observed that pikeperch have a proportionately smaller liver than that of walleye, and that the abdominal musculature of pikeperch appears to be of greater diameter than that of walleye.

The egg diameter of pikeperch ranges from 0.8 to 1.5 mm (Deelder and Willemsen 1964); in contrast, walleye eggs range from 1.4 to 2.1 mm (Miles 1915; Schultz 1971). Consequently, the ratio of surface area to volume is much greater for the pikeperch's egg, averaging 2.9 mm^2/mm^3 as compared with 1.8 mm^2/mm^3 for walleye.

Pikeperch produce a large quantity of these comparatively small eggs, accounting for their greater fecundity than that of walleye. The number of eggs per gram of body weight ranges from 110 to 260 for the pikeperch (J. Willemsen personal communication), and from 20 to 65 for the walleye (Colby et al. 1977).

Physiology

Both species can tolerate a rather great temperature range; however, pikeperch can withstand, and generally prefer, warmer water than do walleye. Temperatures allowing optimum growth range from 28 to 30°C for pikeperch, approximately 5.5 deg. C greater than for wall-

TABLE 1. Selected morphological, physiological, and behavioral characteristics of the walleye and pikeperch, on basis of literature.

Item	Walleye	Pikeperch
	Morphology	
Meristic counts		
Vertebrae	44–48[a]	45–48[ll]
Lateral line scales	83–104[a]	75–150[ll]
1st dorsal spines	XII–XVI[a]	XII–XVII[ll]
2nd dorsal spines/rays	I/18–22[a]	I–III/19–25[ll]
External		
Head length/body length	.261[a]	< .250[mm]
Body depth/body length	.159[a]	.220[nn]
Snout length/head length	.253–.335[a]	.221–.222[nn]
Interobital width/head length	.157–.215[a]	.133–.141[nn]
Eye diameter/head length	.161–.267[a]	.152–.154[nn]
Base of pelvic fin/interpelvic width	.582–.746[a]	1.165–1.397[b]
Body shape in cross section	subterete[b]	strongly subterete[b]
Head shape	relatively blunt[b]	moderately streamlined[b]
Caudal peduncle	relatively slender[b]	deep, robust[b]
Teeth	numerous[b]	less numerous[b]
Tapetum lucidum	great effective area[c]	relatively smaller effective area[c]
Preopercles	posterior edge strongly serrate[b]	posterior edge less serrate[b]
Caudal fin	tips terminate in rounded lobes[b]	tips terminate at sharper angles[b]
Sexual dimorphism	not obvious[a]	ventral surface of female much lighter colored than that of male; genital papilla protrudes in female[mm]
Gill rakers	slender and elongate on outer edge of gill arch, compressed on inner edge[b]	short and robust on both edges of gill arch[b]
Color differences	trunk olive brown, golden brown, or yellow with a darker dorsal surface and white ventral surface; black blotch at posterior-basal portion of 1st dorsal (no spots), lower tip of caudal and tip of anal fin milk white[a]	back and sides greenish to blue-grey, ventral surface white or bluish; black spots on longitudinal rows on dorsal fins, caudal fin spotted in transverse rows, other fins yellowish-grey[oo]
Internal		
Pyloric caeca	3[a]	4–8[mm]
	Physiology	
Water temperature		
Preferred	21–23°C[d]	24°C[d]
Upper incipient lethal	31.6°C[d]	34.3–35.0°C[d]
O_2		
Lower limits	loss of coordination and equilibrium at 0.6 mg/litre[e]	4.5 mg/litre lethal limit for embryos and fry, and lower limit of optimal zone for adults[pp]
Turbidity		
Preferred	intermediate levels[f]	high levels[jj]
Light		
Ambient daylight illumination levels	larvae positively phototactic, adults and subadults negatively phototactic[b,g,h,i]	
	Reproduction	
Maturity		
Initial age	♂2–4 yr ♀3–6 yr[a]	♂2–6 yr ♀3–6 yr[mm]
Size	♂28 cm ♀36–43 cm[a]	♂32 cm ♀42–44 cm[mm]
Fecundity		
Egg no./g body wt	30–65[j]	110–260[mm]
Coefficient of fecundity	10–144[k]	12–144[qq]
Spawning		
Seasons	usually April-May with extremes from late March to late June[h]	usually April-May with extremes from late February to late July[mm,rr]

TABLE 1. *Continued.*

Item	Walleye	Pikeperch
Time of day	throughout night[a]	dawn[mm]
Temperature	normally 8°C range 4.4–14.4°C[l,m]	normally 12°C range 6–18°C[h,mm]
Depth	less than 5 m[n]	as deep as 17 m[ss]
Substrate	sand, gravel, boulders and occasionally vegetation[o]	plant roots or submerged trees on organic, sandy or stony bottom[mm]
Duration	no evidence of protracted spawning[b]	often spawn intermittently over a number of days[tt,uu]
Spawning behavior		
Mating	polygomous, broadcasts eggs[a]	monogamous, redd builder[h,mm,vv]
Postspawning	no protection of eggs[h]	fans eggs, guards nest[h]
Egg		
Egg diameter	1.4–2.1 mm[p,q]	0.8–1.5 mm[mm]
Oil globule diameter	0.8 mm[r]	0.4–0.5 mm[mm]
Surface area/volume	1.8 mm^2/mm^3[s]	2.9 mm^2/mm^3[qq]
Adhesive qualities	agglutinative until water hardened[a]	highly agglutinative until end of incubation[mm]
Resorption of eggs	observed after cold front disrupted spawning activities or during protracted cold spawning period[t,u,v]	
Fertilization		
Success	3–100%[w,x]	63–100%[mm,ww]
By artificial means	practical[y]	difficult and seldom successful[h]
	Embryonic Development	
Incubation period		
At low temp. (6–12°C)	15–34 days[z]	13–26.5 days[mm]
At high temp. (12–24°C)	4–15 days[aa]	4–13 days[mm]
Egg mortality		
Mortality rates	4–82%[o,bb]	5–10%[mm]
Temperature allowing greatest % hatch	9–15°C[z]	12–20°C[mm]
	Larval Development	
First feeding		
Initial diet	diatoms, nauplii, rotifers[cc,dd]	mostly nauplii, some rotifers[mm]
Rate of development		
Length at hatch	6.0–8.6 mm[a]	4.0–5.0 mm[mm]
Length when oil globule and yolk sac resorbed	10.0 mm[ee]	5.8–7.0 mm[mm]
Temperature of optimal growth	20–25°C[d]	28–30°C[d]
Food of postlarvae and juveniles		
Transition diet	progress from diatom-rotifers diet, to microcrustaceans (cladocerans and copepods), then to mixture of microcrustaceans and insect larvae, and finally to fish (yellow perch)[j]	progress from diet of nauplii and copepodites to copepods, then to *Neomysis*, and finally to fish (smelt)[mm]
Behavior of fry		
Schooling behavior	continue to school when piscivorous and through adult stage[o,ff]	school when plankton-feeding but become increasingly solitary when piscivorous[xx]
Factors affecting year-class strength		
Rapid spring temperature increases	positive correlation[v,w,gg,hh,ii,jj]	
	Adult Phase	
Food and feeding		
Feeding habits	opportunistic feeder, cannibalistic[j]	opportunistic feeder, seldom cannibalistic[mm]
Preferred food species	yellow perch (*Perca flavescens*) and cisco (*Coregonus artedii*)[j]	smelt (*Osmerus eperlanus*) and ruffe (*Gymnocephalus cernua*)[mm]
Swallowing of prey	usually head first[b]	often tail first[mm]
Growth		
Growth rates	the two species appear to grow at similar rates in equivalent environmental conditions[h]	

TABLE 1. *Concluded.*

Item	Walleye	Pikeperch
Behavior		
Spawning migrations	often long range; occur throughout the walleye's range[j]	usually short range; occur in isolated areas only[yy,zz]
Daily movements	related primarily to levels of subsurface illumination[b,kk]	
Daytime habitat	under submersed shelter (weed beds, submerged trees, boulders) in clear water; shielded by water column in turbid water[a,kk]	normally shielded by column of turbid waters[b,vv]

[a]Scott and Crossman (1973); [b]Ryder (unpublished data); [c]Moore (1944); [d]Hokanson (1977); [e]Scherer (1971); [f]Ryder (1968); [g]Ali and Anctil (1968); [h]Jovanovic (1970); [i]Toivonen (1966); [j]Colby et al. (1977); [k]calculated from published data, Colby et al. (1977); [l]Herman (1947); [m]Rawson (1957); [n]Baker (1964); [o]Eschmeyer (1950); [p]Schultz (1971); [q]Miles (1915); [r]Whitaker (1890); [s]calculated from published data, Schultz (1971), Miles (1915); [t]Derback (1947); [u]Kukuradze (1968b); [v]Nagiéc (1977); [w]Baker and Scholl (1969); [x]Johnson (1961); [y]Olson (1971); [z]Smith and Koenst (1975); [aa]Anonymous (1967); [bb]Smith and Kramer (1963); [cc]Smith and Moyle (1945); [dd]Hohn (1966); [ee]Nelson (1968); [ff]Hughson and Sheppard (1962); [gg]Baker (1966); [hh]Rudolph and Scholl (1970); [ii]Busch et al. (1975); [jj]Svärdson and Molin (1968); [kk]Ryder (1977); [ll]Gaschott (1928); [mm]Deelder and Willemsen (1964); [nn]Shcherbukha (1968); [oo]Schindler (1957); [pp]Kuznetzova (1955); [qq]calculated from published data, Deelder and Willemsen (1964); [rr]Svärdson and Molin (1973); [ss]Belyy (1962); [tt]Kukuradze (1968a); [uu]Kuznetsov (1970); [vv]Pollet (1959); [ww]Bastl (1969); [xx]Woynarovich (1960); [yy]Neuhaus (1934); [zz]Wiktor (1954).

eye. In addition, the upper incipient lethal temperature is 35°C for pikeperch and only 31.6°C for walleye (Hokanson 1977). The normal spawning temperature is approximately 12°C for pikeperch, with a range from 6 to 18°C (Jovanovic 1970). Walleye generally spawn at cooler temperatures, normally 6.7–8.9°C (Scott and Crossman 1973); however, a range of 4.4–14.4°C has been recorded (Herman 1947; Rawson 1957). Temperatures of 12–20°C allow optimum egg development for pikeperch (Deelder and Willemsen 1964). Similarly, Smith and Koenst (1975) found the greatest percentage hatch of walleye eggs to occur between 9 and 15°C.

In laboratory experiments, walleye have been known to thrive at dissolved oxygen concentrations of 1.5 mg/ℓ and to withstand levels as low as 0.6 mg/ℓ (Scherer 1971). Conversely, the oxygen requirements of pikeperch are relatively high, 4.5 mg/ℓ being recorded as the lower limit of the optimum zone for adults and as the lethal level for both embryos and fry (Kuznetzova 1955).

Both pikeperch and walleye are common in waters of various turbidities and can probably withstand very high concentrations of suspended materials (Wallen 1951). Pikeperch, however, seem to prefer somewhat more turbid conditions than do walleye (Jovanovic 1970).

Ethology

Adult walleye are negatively phototactic to ambient levels of subsurface illumination and during the daylight hours seek some form of physical shelter, such as boulders, weed beds, sunken trees, and other types of submerged debris (Ryder 1977). Pikeperch are also negatively phototactic as adults, but to a lesser degree than walleye due to a reduction in the effective area of the tapetum lucidum (Moore 1944; Toivonen 1966). There have been isolated reports of pikeperch seeking physical cover (Pollet 1959); however, it appears this species generally makes use of the differential in turbidity levels and simply descends in the water column to avoid excess illumination.

The feeding transition is similar for both species from larva to adult (Table 1), at which time they become opportunistic feeders preying mainly on fish. Data collected by W. J. Scidmore (personal communication) suggests that young-of-the-year and yearling walleye ingest their prey tail-first, however, adult walleye have been observed to always seize their prey from the side, and gradually work it around in their mouths until it can be swallowed headfirst (R. A. Ryder unpublished data). Pikeperch seize their prey in a haphazard manner, usually from the side or tail, particularly in the case of smelt (*Osmerus eperlanus*). N. P. Van Zalinge (unpublished data) reported that in the Tjeukemeer adult pikeperch ingest their prey headfirst; however, over most of their range they have been observed to swallow at least some species tailfirst (Neuhaus 1934; Steffens 1960; R. A. Ryder unpublished data). R. A. Ryder (personal communication) suggests that this phenomenon may be attributed to the absence of elongated gill rakers in pikeperch, which if present (as in adult walleye), would tend to snag on protruding fins and opercula of their prey. In addition, it is suspected that all spiny-rayed specimens must be oriented headfirst before ingestion to prevent spines or the preopercles from lodging in the pikeperch's buccal cavity and esophagus.

Cannibalism among walleye has been observed over most of their range and appears to be a principal source of mortality for walleye fry when the density of forage species is low (Chevalier 1973; Forney 1974). Occurrences of pikeperch cannibalism have been reported when young of its own kind were abundant and other prey fish were scarce (Steffens 1960; Willemsen 1977), however, pikeperch are generally less cannibalistic than walleye (R. A. Ryder unpublished data). This is clearly evident when examining the ease in which pikeperch are raised in hatchery ponds; a practice usually proving difficult for walleye due to high rates of cannibalism.

Pikeperch exhibit schooling behavior while feeding on zooplankton, but become increasingly solitary as they reach the piscivorous stage (Woynarovich 1960). Walleye, however, continue to school as they become piscivorous (Eschmeyer 1950) and form schools even as adults (Ryder 1977).

No distinct seasonal migratory habits have been discovered that are valid for the whole range of the pikeperch's distribution (Deelder and Willemsen 1964) although isolated cases have been described throughout Eurasia: Nikol'skii (1940), for Aral Sea pikeperch; Puke (1951) and Rundberg (1977) for pikeperch in Swedish Lakes; Tanasiychuck et al. (1954), for Volga pikeperch; Toivonen (1969), for Baltic pikeperch; and Willemsen (1977), for Ijsselmeer pikeperch. On the other hand, mature members of all self-propagating walleye populations, whether stream or lake-spawning, migrate from their overwintering grounds to their spawning grounds in spring and continue to their summer feeding grounds shortly after spawning (Ryder 1968; Colby et al. 1977). J. Thorpe (personal communication), however, suggests that this may not be such an obvious difference, but instead a function of the relative scarcity of large water bodies in the pikeperch's range, limiting the distance available for travel, and thereby making any migration less noticeable.

Balon (1975) considered pikeperch and walleye to belong to divergent ecoethological guilds based on their reproductive behavior. Walleye belong to the nonguarding, open-substrate spawning lithophil guild, whose members are adapted to well-oxygenated waters and have moderately developed respiratory organs. Pikeperch are members of the guarding, nest-spawning, phytophil guild. These fish are adapted to nesting above or on a soft organic bottom with low oxygen concentrations and a high oxygen demand.

The male pikeperch build more or less elaborate redds by excavating a round pit until the roots of submerged plants become exposed (Deelder and Willemsen 1964). The eggs are then deposited above the bottom on these plant roots, or submerged trees or various other objects exposed within the redd, where they remain until the end of incubation due to their highly agglutinative qualities. In contrast, walleye simply broadcast their eggs across a large area of unguarded substrate, usually consisting of rock, rubble or gravel. This nesting behavior results in a consistently greater fertilization rate for pikeperch, ranging from 63 to 100% (Deelder and Willemsen 1964; Bastl 1969). Johnson (1961) and Baker and Scholl (1969) report the percentage of fertilized walleye eggs to be quite variable — from 3 to 100%.

The male pikeperch guards the redd up to the early fry stages, allowing little predation on the eggs. In addition, it fans the eggs with its pectoral fins, creating water currents around them. Walleye provide no parental protection whatsoever, leaving their eggs vulnerable to predation. Hence, egg survival for pikeperch is high, with losses not exceeding 5 to 10% under normal circumstances (Deelder and Willemsen 1964), whereas up to 82% mortality of fertilized walleye eggs has been recorded (Colby et al. 1977).

Pikeperch seem to require a less rigorous set of spawning conditions than walleye. Viable pikeperch eggs have been collected as deep as 17 m (Belvy 1962), whereas the maximum depth at which walleye spawn is 4.6 m (Baker 1964). Both species are spring spawners; however, in contrast to walleye, pikeperch often spawn in batches over a protracted period of time (Kukaradze 1968a; Bastl 1969; Kuznetsov 1970). This increases the likelihood of survival of at least some offspring as some eggs of an individual would probably hatch during optimum conditions.

Adaptations of Pikeperch to Culturally Advanced Trophic Systems and Reservoirs

The preferred biotope of pikeperch can be characterized as moderate to relatively warm, productive waters, stagnant or slowly running, with a high turbidity. Waters with these attributes are usually considered as advanced mesotrophic to eutrophic in nature. Walleye generally inhabit cooler, less turbid, mesotrophic waters although early eutrophy may be tolerated in special circumstances. Various adaptations have evolved which enable pikeperch to tolerate the conditions associated with enhanced productivity and compete in such an environment.

The high reproductive potential of pikeperch offsets effects of the catastrophic change in the composition of the fish community that may occur (Kerr 1977) as lakes eutrophy. Members of the family Cyprinidae, among others, become increasingly abundant, and some of these species are known to prey on pikeperch eggs and larvae as well as to compete directly with pikeperch fry for food and space. As a counter-measure pikeperch have developed a relatively great rate of reproduction, attributable to a high fecundity, consistently successful fertilization, lowered mortality of eggs and larvae, and less rigorous spawning requirements.

Several adaptations of genetic nature have transpired which allow pikeperch to cope with accumulations of silt and seston on their spawning grounds and oxygen deficiencies in the lower strata, produced through nocturnal respiration and decomposition of large algal blooms common in eutrophic systems. The relatively great ratio of surface area to volume of the pikeperch's egg allows for a more efficient gas exchange between the developing egg and the surrounding water. Behavioral adaptations include the deposition of spawn above the anoxic bottom-water interface on plant roots and other submerged objects exposed within the nest, and fanning of the eggs to remove debris and create a continuous water exchange about them. As the majority of pikeperch populations do not undergo distinct spawning migrations these responses may be sufficient to overcome abiotic variation of spawning sites from one year to the next, and may be analagous to the extensive spawning migrations of walleye, which have been termed (Harden Jones 1968) a behavioral adaptation allowing for the maintenance of a larger population by ensuring that spawning occurs only in areas with optimum conditions.

Both species have a well-developed tapetum lucidum which enhances their vision in waters of high organic turbidity, a condition common to advancing eutrophication due to dense growths of green and blue-green algae. However, the effective tapetal area is relatively larger in the walleye, indicating greater visual acuity under reduced light intensities (Moore 1944). This reduction in area may make the pikeperch a less efficient predator in the turbid waters it normally inhabits, particularly during crepuscular or nocturnal feeding forays. Conversely, however, tapetal reduction may enable this species to function at higher subsurface illumination levels and perhaps explains the pikeperch's ability to feed during daylight hours (Jovanovic 1970) while the walleye's feeding activity is generally limited to dusk or dawn (Ryder 1977).

The critical factor limiting the pikeperch's survival in eutrophic waters is apparently its high oxygen requirement, resembling that of salmonids more than the other percids (Toivonen 1966). However, this high oxygen demand may be compensated for by vertical displacement in the water column, as the more light-tolerant pikeperch are capable of inhabiting the oxygen-rich surface waters (R. A. Ryder unpublished data). Supporting this proposal, Wundsch (1963) reported that pikeperch thrive in waters which show a seasonal oxygen shortage, provided that this shortage does not occur in the topmost 4 to 6 m of water.

Pikeperch have the ability to spawn in much deeper waters and over a much wider array of bottom types than do walleye. Consequently, they are able to tolerate the frequent and wide variations in water levels common to reservoirs. This has been demonstrated in research by Bastl (1969) on the Orava Reservoir in northern Czechoslovakia and Kuznetsov (1970) on the Kuybyshev Reservoir in central Russia, where pikeperch have become an important commercial species. The wide adaptability in choice of spawning grounds has enabled pikeperch to avoid the littoral areas and make use of the open zones of reservoirs under conditions of regulated river discharge. Similarly, in the Netherlands, Willemsen (1977) reported a relatively high catch per hectare for pikeperch in the Ijsselmeer, transformed from a marine bay (Zuiderzee) to a lake in 1932, even though the lake has been reduced to one third of its original area due to the construction of polders. Walleye have become successful in reservoirs only when tributaries suitable for spawning exist, and the problem of fluctuating water levels can be avoided, or when water levels remain relatively constant (Machniak 1975).

In summary, the pikeperch, described by Toivonen (1966) as among the most important of the eutrophication-tolerant fishes, can withstand a wider range of environmental conditions and tolerate alterations of its habitat to a much greater degree than the walleye. For these reasons pikeperch may prove to be suitable species for introduction under adverse conditions not likely to be rectified and unsuitable for native species.

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Temperature Requirements of Some Percids and Adaptations to the Seasonal Temperature Cycle[1]

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HOKANSON, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524–1550.

Temperature requirements are reviewed for three North American percids (walleye, *Stizostedion vitreum vitreum*; sauger, *S. canadense*; and yellow perch, *Perca flavescens*), three Eurasian percids (perch, *P. fluviatilis*; pikeperch, *S. lucioperca*; and ruffe, *Gymnocephalus cernua*), and nine cohabitant fish species for comparison. Whole-organism responses are described for each species — primarily concerning reproduction, growth, survival, and activity. The percids are classified as temperature mesotherms and they are arranged in order of their thermal requirements as follows: pikeperch > perches and ruffe > sauger > walleye. *Perca* and *Stizostedion* spp. are annual spawners with synchronous oocyte growth during fall through winter, culminating in spring spawning. Maturation occurs below 12°C. Spawning occurs from late February through early July at 2–26°C over their geographic ranges. Oocyte growth of ruffe is asynchronous, accelerated by warm temperatures; batch spawning occurs over a prolonged period, from mid-April through July at 11–18°C. Physiological optima range from 22°C for sauger and walleye to 25°C for perch and 27°C for pikeperch. The ultimate upper incipient lethal temperatures of percids range from 29 to 35°C, depending on species and experimental conditions.

Percid life phases are uniquely adapted to the seasonal temperature cycle of a temperate climate. The maturation limit (10°C) for *Perca* spp. approaches the minimum winter temperature in lowermost latitudes of their distribution. Increasing temperature requirements of successive early life phases show how percids adapt to the spring spawning period. Spawning begins in a temperature range that optimizes gamete viability. Temperature has little effect on duration of the phases of gonad maturity in *Perca* and *Stizostedion* spp. These fishes adapt to different temperature regimens by shifting spawning temperatures, while spawning time changes only slightly, sometimes at the expense of gamete viability. Greater differences in spawning time observed at geographical extremities of their range are believed to be due to longer term adaptations that determine time of first maturity rather than adaptations of the adult maturation cycle. Ruffe are more adaptable, spawning several batches of ova under favorable environmental conditions. Summer distributions of *Perca* spp. lie between the 16 and 31°C isotherms. These values represent the lower limit to normal maturation of adults and growth of young and the upper temperature for zero net biomass gain, respectively. Only maximal temperatures in lower latitudes approach the ultimate upper incipient lethal temperature of a species. Fish adapt to different thermal characteristics by changes in their avoidance/preference response, diel activity cycles, and seasonal migrations. No uniform mechanism of population regulation or resiliency is apparent for different acclimatization conditions. Therefore, management regulations for a given species should not be universally applied throughout its geographic range.

Key words: Percidae, temperature requirements, adaptations, seasonal temperature cycles, *Perca*, *Stizostedion*, *Gymnocephalus*, temperature classification, literature synthesis

HOKANSON, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524–1550.

Nous passons en revue les exigences thermiques de trois percidés nord-américains (le doré jaune, *Stizostedion vitreum vitreum*; le doré noir, *S. canadense*; et la perchaude, *Perca flavescens*), trois percidés eurasiens (la perche, *P. fluviatilis*; le sandre, *S. lucioperca*; et la perche goujonnière, *Gymnocephalus cernua*), que nous comparons avec celles de neuf espèces de poissons habitant les mêmes milieux. Nous décrivons pour chaque espèce les réponses de

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l'organisme entier — principalement celles touchant la reproduction, la croissance, la survie et l'activité. Nous classifions les percidés comme mésothermes tempérés et les disposons par ordre d'exigences thermiques comme suit: sandre > perches et perches goujonnières > doré noir > doré jaune. *Perca* et *Stizostedion* spp. fraient annuellement, avec croissance synchrone des ovocytes en automne et durant tout l'hiver, culminant avec la ponte au printemps. La maturation se produit à une température inférieure à 12°C. La fraie a lieu depuis la fin de février jusqu'au début de juillet à 2–26°C dans l'aire de toutes les espèces. La croissance des ovocytes de la perche goujonnière est asynchrone, étant accélérée par de chaudes températures; la fraie par lots se produit sur une longue période, de la mi-avril à juillet inclusivement à 11–18°C. Les optimums physiologiques vont de 22°C pour le doré noir et le doré jaune à 25°C pour la perche et 27°C pour le sandre. Les températures supérieures ultimes du début des mortalités des percidés varient de 29 à 35°C, selon l'espèce et les conditions expérimentales. Les phases de la vie des percidés sont adaptées de façon unique au cycle de températures saisonnières d'un climat tempéré. La limite de maturation (10°C) de *Perca* spp. se rapproche du minimum de température d'hiver aux plus basses latitudes de leur distribution. Les exigences thermiques croissantes des phases successives du début de la vie montrent comment les percidés s'adaptent à la période printannière de fraie. La fraie commence à une gamme de températures qui donne une viabilité optimale des gamètes. La température a peu d'effet sur la durée des phases de maturation des gonades chez *Perca* et *Stizostedion* spp. Ces poissons s'adaptent à différents régimes de température en déplaçant les températures de fraie, alors que la période de fraie ne change que légèrement, parfois au dépens de la viabilité des gamètes. On croit que les plus grandes différences dans la période de fraie observées aux extrémités géographiques de leur aire sont dues à des adaptations à plus long terme qui déterminent l'époque de la première maturité, plutôt qu'à des adaptations du cycle de maturation adulte. La perche goujonnière est plus adaptable, pondant plusieurs lots d'œufs quand les conditions ambiantes sont favorables. La distribution estivale de *Perca* spp. se situe entre les isothermes de 16 et 31°C. Ces valeurs représentent la limite inférieure d'une maturation normale des adultes et d'une croissance des jeunes, et la température supérieure pour un gain nul de biomasse nette, respectivement. Seules les températures maximales aux basses latitudes se rapprochent de la température supérieure ultime du début des mortalités d'une espèce. Les poissons s'adaptent à différentes caractéristiques thermiques en changeant leur réponse d'évitement/préférence, leur cycle nycthéméral d'activité et leurs migrations saisonnières. Il ne semble pas y avoir de mécanisme uniforme de réglage ou de résistance des populations sous différentes conditions d'acclimatation. Les règlements concernant la gestion d'une espèce donnée ne devraient donc pas être universellement appliqués dans toute son aire géographique.

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THE purpose of this review is to describe the temperature requirements and adaptations to the seasonal temperature cycle of some commercially important freshwater percids: the walleye (*Stizostedion vitreum vitreum*), sauger (*Stizostedion canadense*), and yellow perch (*Perca flavescens*) of North America and the perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*), and ruffe (*Gymnocephalus cernua*) of Eurasia. The temperature requirements of nine cohabitant species are described for comparison so that a temperature classification scheme could be developed for percids and other freshwater fishes. The present range of self-sustaining populations of these percids extends from about 30 to 75° N lat. (Weatherley 1963a; Deedler and Willemsen 1964; Berg 1965; Scott and Crossman 1973). The species are adapted to temperate climates of the northern hemisphere, although perch were successfully introduced into Australia. Water temperatures in percid habitat vary seasonally from <4°C for more than 8 mo in the northernmost latitudes to about 32°C in the southernmost extremities of the percid range.

As PERCIS evolved from management's needs for information on exploitation, habitat modification, and rehabilitation of percid communities, this paper is limited to whole-organism responses — specifically reproduction, growth, survival, and activity. These responses encompass the effects of temperature on the physiology of fishes, are most readily measured in field-stock assessment, and are important parameters in population-dynamics models of yield and production which can be used to evaluate man-imposed stresses.

The temperature requirements of these percids are described for each response. Seasonal changes in thermal responsiveness of percids are of special interest because they modify the effects of temperature on different phases of the life cycle, maturation cycles, spawning times, migrations, activity, and ultimately distribution and abundance of the species. I describe effects of temperature on percids from several unpublished

TABLE 1. Temperature classification of temperate-climate[a] freshwater fish.

Classification	Criteria	Species
Temperate stenotherm	Gonadal growth phase in summer, <20°C	Brook trout (*Salvelinus fontinalis*)
	Spawning in fall to spring, <15°C	Rainbow trout (*Salmo gairdneri*)
	Physiological optimum, <20°C	Lake herring (*Coregonus artedii*)
	Ultimate upper incipient lethal temp, <26°C	
Temperate mesotherm	Gonadal growth phase in fall and winter, <12°C	White sucker (*Catostomus commersoni*)
	Spawning in spring, 3–23°C	Northern pike (*Esox lucius*)
	Physiological optimum, 20–28°C	Percids reviewed herein
	Ultimate upper incipient lethal temp, 28–34°C	
Temperate eurytherm	Gonadal growth phase during long days, >12°C	Largemouth bass (*Micropterus salmoides*)
	Spawning in spring to fall, 15–32°C	Bluegill (*Lepomis macrochirus*)
	Physiological optimum, >28°C	Tench (*Tinca tinca*)
	Ultimate upper incipient lethal temp, >34°C	Carp (*Cyprinus carpio*)

[a] The use of the term *temperate* as a prefix in classification represents the ability of most temperate-climate species to survive temperatures near freezing (<4°C). Therefore, description of a species' thermal requirements reflects their relative biokinetic range of tolerance, performance, and activity.

papers within my organization to establish percid requirements, since key information on reproduction and activity is lacking. Graphical endpoints from experimental data are defined so that temperature relationships among percids and cohabitant species can be compared. Standardized methods were not used. Therefore, I describe the effects of experimental factors to explain variation in temperature responses and to facilitate comparisons among species. Natural-history observations supplement experimental data where appropriate. Species of *Perca* have been studied most often; comparable data are rather sparse for other percids, particularly Eurasian species. Therefore, temperature requirements of *Perca flavescens* and *P. fluviatilis* are compared with temperature limits of distribution to establish the physiological and ecological significance of graphical endpoints used herein. These comparisons suggest several adaptive mechanisms to the seasonal temperature cycle. Based on autecology relationships, I suggest a hypothesis concerning percid population adaptations to different temperature regimens that may have useful management implications.

Temperature Classification

Percids can be classified as temperate mesotherm, which reflects the intermediate temperature niche of percids in fish communities. A classification scheme is needed that recognizes the species with intermediate requirements, especially among the warmwater species. The use of the term *temperate* as a prefix in classification represents the ability of most temperate-climate species to survive temperatures near freezing (<4°C). Therefore, description of a species' thermal requirements reflects their relative biokinetic range of tolerance, performance, and activity. A temperature classification scheme that recognizes three limits of thermal requirements and modes of reproduction is proposed for temperate-climate species (Table 1). Temperate stenotherms include *Salvelinus fontinalis*, *Salmo gairdneri*, and *Coregonus artedii*; other temperate mesotherms include *Catostomus commersoni* and *Esox lucius*, which are commonly associated with percids; and temperate eurytherms include *Micropterus salmoides*, *Lepomis macrochirus*, *Tinca tinca*, and *Cyprinus carpio*. Further classification is not warranted until the temperature requirements of various species and life phases are accurately described on the basis of uniform criteria and procedures.

Percids may be associated with warm- and coldwater species. In cold-water lakes percids occupy the surface waters and embayments, whereas cold-water Salmonidae occupy the deeper offshore areas (Hile and Juday 1941; Echo 1955; McCormack 1965; Ryder 1968; Thorpe 1974). Percids are known to feed on cold- and warmwater species. Percids were confined to deeper water in summer in southernmost latitudes, and species adapted to warmer water were in the surface waters (Dendy 1948). Depth distribution in these waters can be limited by warm surface waters and low dissolved oxygen concentrations in the hypolimnion. Percids are generally among the less abundant species around thermal plumes in all seasons of the year (Alabaster and Downing 1966; EIFAC 1968; Boytsov 1971; Gammon 1971; Horoszewicz 1973; Neill and Magnuson 1974).

Percids can be arranged in the following order of thermal requirements: pikeperch > perches and ruffe > sauger > walleye. Pikeperch clearly have higher thermal requirements for all responses than the perches. Sauger and walleye have distinctly lower physiological optima and lethal temperatures than the perches. Walleye require lower temperatures for spawning than the sauger, which is the principal difference between the two species. On the basis of available data, one cannot distinguish between the temperature requirements of Eurasian perch, yellow perch, and ruffe. Successful hybridization between ruffe and Eurasian perch also suggest similarities between the two species (Kammerer 1907). These subtle differences in thermal tolerance may be reflected in their geographical distribution.

Experimental conditions can be a greater source of variation than specific differences among percids. A difference in thermal response between two stocks does not imply genotypic variation (Fry 1957). No racial differences in thermal tolerance have been demonstrated for a wide variety of fishes from isolated habitats and different thermal regimens (Hart 1952; Brown and Feldmeth 1971; Horoszewicz 1973). Hubbs (1971) noted that walleye eggs from Lake Meredith, Texas (introduced from Iowa), developed at 20°C, whereas eggs from the Thames River, Ontario, had poor survival at 16.5°C. He suggested that there were racial differences in thermal tolerance. However, he did not account for differences in egg quality as influenced by fertilization temperature, which also contributes to the percentage of eggs that hatch. Lack of comparable experimental data does not imply that no racial differences exist. Other attributes besides temperature tolerance, such as light sensitivity, bioenergetics, maturation rate, swimbladder adaptations to depth, feeding, and migratory behavior, may separate a species along a habitat gradient.

Reproduction

Fish reproduction involves a complex sequence of events, including gonad growth and gamete maturation, spawning migration, release of viable gametes, embryo and larval development, and the beginning of independent feeding by larvae. Fishes of the temperate climate respond to regular seasonal cycles of temperature and day length. Such rhythms ensure maturation and spawning at regular times in each locality. The critical temperatures that permit successful maturation, spawning, and gamete viability are of special interest to this review.

Maturation cycle — *Perca* and *Stizostedion* spp. have synchronous oocyte growth and are annual spawners that lay all their eggs at one time in shallow water in the spring (Koshelev 1963; Breder and Rosen 1966). Turner (1919) described the seasonal cycle in the spermary of yellow perch from Lake Mendota, Wisconsin: the testis was smallest from late June to late August, which is a period of germ-cell migration, proliferation, and growth, and maximum water temperature. The volume of the testis began to increase in September and reached maximum size in early November. Spermatids and spermatozoa began to form in early September and remained in the mature stage until spawning in the spring. The increase in testicular volume and beginning of spermatogenesis were contemporaneous with the beginning of a seasonal decrease in water temperature. Testicular volume declined rapidly from March through June as spermatozoa were expelled during spawning in a period of rising water temperature. LeCren (1951) observed a similar testicular cycle in the Eurasian perch from Lake Windermere, England.

The principal growth phase of the ovaries of *Perca* and *Stizostedion* spp. takes place during the coolest seasons, when body growth ceases. Koshelev (1963) described the seasonal oogenesis cycle in Eurasian perch from Lake Glubokoe, USSR, and LeCren (1951) described the seasonal cycle in the ovary–body-weight ratio of perch from Lake Windermere, England, as follows: after the fish spawns, the ovaries pass into a transitional stage of maturity (stage VI–II), which generally lasts for a month, and is characterized by resorption of the remnants from the emptied follicles. The ovary–body-weight ratio declines from 3 to 1% of the body weight during this period. A period of no ova growth but active oogenesis (stage II) lasts from the middle of June through August. The active growth phase of the ova and development of numerous vacuoles (stage III) lasts 45–60 days, from early September to late October. The start of formation of fat and yolk in the oocytes (stage IV) begins in November. Synchronous growth of oogonia continues until spawning in May when the ovary averages 20% or more of the body weight. The total period of active ova growth and vitellogenesis lasts about 220 days in perch. In contrast, ovulation and spawning (stage V) last for only a few days. Maturation cycles similar to Eurasian perch have been observed for yellow perch from Lake Michigan (Brazo 1973), walleye from Lake Ontario (Payne 1964), and pikeperch from the USSR (Golovanenko et al. 1970).

Resorption of oocytes or lengthening the post-spawning stage (VI–II) due to unfavorable conditions of the habitat can interfere with development of the next year's batch of oocytes in fish with synchronous oocyte growth (e.g. *Perca* and *Stizostedion* spp.). Deficiency in food and poor growth conditions in summer can reduce the rate of the resorptive processes and delay the period of oocyte growth sufficiently to cause them to miss the following spawning period (Eschmeyer and Smith 1943; Koshelev 1963; Forney 1965; Scott and Crossman 1973). Delayed or interrupted spawning seasons can lead to resorption of ova in walleye (Derback 1947; Schumann 1964) and pikeperch (Golovanenko et al. 1970). A large number of Eurasian perch failed to spawn after unusually severe winters in Windermere, England (LeCren 1965). Ova resorption interferes with development of the next batch of oocytes in pikeperch (Kukuradze 1968) and walleye (W. B. Horning II, U.S. EPA, Newton, Ohio, personal communication), which prevents reproduction in the following spawning period. Growth of the new batch of oocytes begins in these species only after completion of all the resorptive processes in the ovary (Koshelev 1963).

Ruffe are more adaptable to changing environmental conditions than *Perca* and *Stizostedion* spp. In ruffe, oocyte growth is asynchronous and spawning is intermittent (Koshelev 1963). Ruffe differ from the other percids in having a faster oocyte growth rate in the period of fat and yolk accumulation in spring and early summer and less oocyte growth over winter. The first batch of oocytes matures (stage III–V) in 165 days during winter and spring and the second in 30 days during summer. The faster oocyte growth rate during vitellogenesis leads to maturation of several batches of oocytes during the year and prolongs the spawning period where conditions are more favorable. Stage II is absent and oocytes are in various stages of development or resorption throughout the spawning period. Resorption of unspawned ova does not interfere with growth of the next batch of oocytes because ova growth and resorption occur simultaneously in this species (Koshelev 1963).

Maturation requirements — a winter minimum temperature of 10°C is near the upper limit for maturation of gonads in yellow perch and walleye. Jones et al. (1977) reared adult yellow perch from Minnesota in the laboratory under a natural day-length cycle and 16 thermal regimes from October through June. The maximum percentage of females spawning declined as the winter minimum temperature at which they had been held increased (Fig. 1). Optimal conditions for maturation that terminated in spawning occurred when fish were exposed to 6°C or lower for 185 days from October 30, whereas no viable spawning occurred when the fish were maintained at a minimum temperature of 12°C or higher. In preliminary studies, viable spawnings were observed among perch held at a minimum of 12°C except for 1½ mo at 8°C in winter. Chill durations <185 days from October 30 reduced spawning in these treatments. High temperatures at the end of these treatments may have blocked maturation or spawning. Miller (1967) reported that introduced walleye failed to reproduce in California reservoirs. These waters became essentially isothermal in winter at temperatures ranging from 10 to 12.5°C (G. W. McCammon, Department of Fish and Game, Sacramento, Calif., personal communication). Higher temperatures are apparently required for maturation of ruffe, as indicated by rapid development of their oocytes in summer (Koshelev 1963).

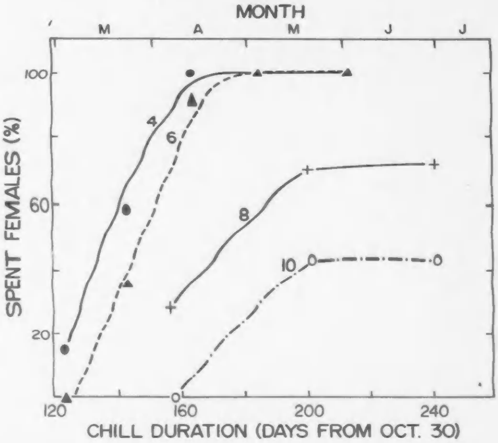

FIG. 1. Percentages of female yellow perch (*Perca flavescens*) that spawned during exposure to four chill temperatures (4, 6, 8, and 10°C) of different durations (123–242 days from October 30). Temperature was increased at a rate of 2°C/wk to a maximum of 20°C after termination of the exposure to the various chill temperatures (from Jones et al., Environmental Research Laboratory–Duluth, unpublished data).

Time of spawning — Percids spawn during periods of rising temperature in the spring. The rapid adjustment of introduced species to new temperature regimes suggests that spawning time is strongly influenced by local environmental factors and that each stock has a different reproductive cycle. Seasonal changes in day-length and temperature cycles set finite limits on the length of the spawning season for a given fish stock by influencing maturation and ova viability (Hokanson and Biesinger 1977). Upon completion of maturation, spawning is triggered by heterogenous stimuli, such as a rising water temperature, suitable spawning substrate, and courtship behavior (Deelder and Willemsen 1964). Yellow perch exposed to various thermal treatments, previously described, spawned from April 12 to June 20 (Jones et al., Environmental Research Laboratory-Duluth, unpublished data). Of all viable spawnings, 80% occurred during the normal spawning season of this stock, from May 10 to June 8. Yellow perch exposed to warmer thermal regimes spawned only slightly earlier and at somewhat higher temperatures than those exposed to colder temperatures (Fig. 2). For chill durations longer than 214 days, spawning began before termination of the chill period at low constant temperatures; rising temperatures were not required to trigger spawning. Thus, spawning temperature appears to be a function of the prevailing water temperature at the time each stock completes maturation and ovulation.

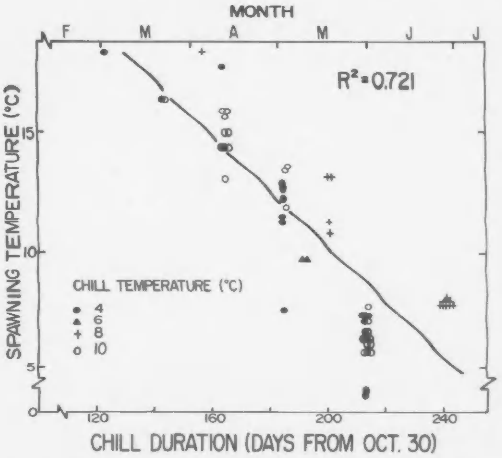

FIG. 2. Spawning temperature observed at the time of laboratory spawning of yellow perch from Minnesota that had been exposed to four chill temperatures for various periods (from Jones et al. Environmental Research Laboratory–Duluth, unpublished data). Chill duration was the time of exposure to chill temperatures from October 30 to beginning of spring rise in temperature at 2°C/wk.

Percids show a greater difference in spawning time at geographical extremities of their range than for any given stock. Although *Perca* and *Stizostedion* spp. may spawn for only 1–3 wk in any given locality, they spawn from late February to early July in different localities (Table 2). Spawning of Eurasian perch in lower latitudes occurs earlier in the year at higher temperatures than in higher latitudes (Thorpe 1977). In reproducing populations of Eurasian perch that have been established in the southern hemisphere, the fish spawn from late August to October during the rising temperature period (Lake 1959). The importance of the temperature regimen in timing of spawning was further emphasized in Turkey, where pikeperch were introduced into two lakes with different temperature regimes. Spawning occurred in late February and March in the lake with the higher temperature, and as late as May–June in the colder lake (Aksiray 1961). Ruffe spawn one to three batches of ova over a 2-mo spawning season in Lake Glubokoe, USSR (Koshelev 1963); they spawn from mid-April through July over their geographic range (Table 2).

Spawning temperature and gamete viability — Percids spawn at temperatures that enhance gamete viability. Smith and Koenst (1975) acclimated mature walleyes to six temperatures from 6 to 21°C. After the fish became ripe, they were stripped and the eggs were fertilized at their respective acclimation temperatures. The eggs fertilized at each acclimation temperature were incubated at each of six incubation temperatures from 6 to 21°C to separate the effects of acclimation (parental) temperature and incubation (embryo) temperature on the hatchability of eggs. The effect of incubation temperature on hatchability was modified substantially by acclimation (parental) temperature (Fig. 3). The principal effect of acclimation temperature was on gamete viability, which was highest at 6–9°C, the temperature range most frequently observed on the spawning grounds. Independent of the effect of fertilization temperature, the highest percentage hatch was at incubation temperatures of 9–15°C.

Yellow perch held at various treatments produced viable ova at temperatures from 3.9 to 18.6°C (Jones et al., Environmental Research Laboratory-Duluth, unpublished data). Eighty percent of all viable spawnings were produced at temperatures from 6.2 to 16.0°C. Gamete viability was highest at 8–11°C.

TABLE 2. Relationships between median temperature tolerance limits of embryos and water temperatures observed on spawning grounds of various percids.

Species	Embryo TL50 (°C)[a]		Spawning temp (°C)[b]		Spawning date[b]	
	Lower	Upper	Lowest	Highest	Earliest	Latest
Walleye (*S. v. vitreum*)	<6.0	19.2[d]	2.2 (Wis.)[i]	15.6 (Wis.)[i]	Mar. 10 (Okla.)[r]	Late June (Can)[v]
Sauger (*S. canadense*)	6.0	>20.9[d]	4 (N. Dak.)[j]	14.4 (Tenn.)[p]	Mid-Mar. (Ala.)[s]	June 25 (N. Dak.)
Yellow perch (*P. flavescens*)	6.8	19.9[e]	2.0 (Md.)[k] 3.9 (Minn.-Lab)[l]	18.6 (Minn.-Lab)[l]	Late Feb. (Md.)[k]	Early July[w] (Lake Mich.)
Eurasian perch (*P. fluviatilis*)	6.1	20.2[f]	5 (USSR)[m]	18.0 (Pol.)[q] 19.0 (Czech.)[n]	Late Feb. Late Aug. (Aust.)[t]	July (USSR)[x]
Ruffe[c] (*G. cernua*)			11.6 (Czech.)[n]	18 (Neth.)[aa]	Apr. 17 (Austria)[u]	Late July (USSR)[y]
Pikeperch (*S. lucioperca*)	10.0 9.0	21.5[g] 24.0[h]	4.5 (USSR)[o]	26 (Finl.)[o]	Late Feb. (Turk.)[h]	Early July (USSR)[z]

[a] Median tolerance limits based on normal hatch of eggs incubated at constant temperature from fertilization to hatch.

[b] Location indicated in parentheses.

[c] Available references limited; therefore, data are common values observed rather than extremes.

[d] Smith and Koenst (1975); [e] Hokanson and Kleiner (1974); [f] Swift (1965); [g] Muntyan (1967); [h] Deelder and Willemsen (1964); [i] Priegel (1970); [j] Carufel (1963); [k] Muncy (1962); [l] Jones et al. (Environmental Research Laboratory-Duluth, unpublished data); [m] Kovalev (1973); [n] Bastl (1969); [o] Zhdanova (1966); [p] Gordon Hall, TVA, Norris, Tenn., personal communication; [q] EIFAC (1968); [r] Grinstead (1971); [s] Wrenn (1974); [t] Weatherley (1963a); [u] Kammerer (1907); [v] Scott and Crossman (1973); [w] Brazo (1973); [x] Berg (1965); [y] Koshelev (1963); [z] Rizvanov (1970); [aa] Willemsen (1977).

Both species of perch spawn at temperatures from 4 to 19°C throughout their geographic ranges (Table 2). Walleye (2.2–15.6°C) and sauger (4–14.4°C) have the lowest spawning temperatures and pikeperch (4.5–26°C) has the highest. Spawning data for ruffe are rather sparse and represent only common values observed on the spawning grounds. In Lake Ilmen, USSR, ruffe and perch usually spawn at about the same time, before pikeperch (Kovalev 1973).

Favorable spawning temperatures may enhance gamete viability through production of specific gonadotropins, which completes maturation and induces ovulation. In contrast to the long growth phase of maturation in *Perca* and *Stizostedion* spp., ovulation or initiation of resorption takes place within 1–3 days, depending on conditions prevailing on the spawning grounds (Koshelev 1963; Golovanenko et al. 1970). Mature females that migrate towards the spawning grounds at temperatures near their lower spawning threshold do not yield viable ova initially, but become fully ripe later in the migration or on the spawning grounds (Deelder and Willemsen 1964; Priegel 1970; Johnson 1971). During the final 2 wk of the maturation cycle of pikeperch, the quantity of protein in the ovary increased 89%, blood hemoglobin decreased 20%, serum protein decreased 21%, protein content of the liver decreased 19%, and lipid content of the liver decreased 34% (Golovanenko et al. 1970). This period coincided with the rise of temperature to the optimum spawning temperature during the migration. Use of gonadotropin injections on female pikeperch at this time is known to hasten the terminal stages of maturation and induce ovulation of matured oocytes (Putina et al. 1970). Balandin (1941) reported that pikeperch that were given a pituitary injection and then released into ponds spawned at 5–8°C, which was below the temperature at which they normally reproduced. The induced ripening of fish at temperatures below the critical ones by means of injection of gonadotropin is a strong indication that a deficiency of gonadotropin is responsible for the cessation of gametogenesis at low temperatures (Atz 1957), and possibly at higher temperatures as well.

Embryonic and larval requirements — Successive early life phases of *Perca* and *Stizostedion* have temperature requirements that increase with morphological differentiation. The temperature requirements of yellow perch are illustrated in Fig. 4. The median tolerance limits (TL50) of successive embryonic and larval phases of yellow perch reported by Hokanson and Kleiner (1974) were 3.7–21°C in early embryonic stages (fertilization to neural keel) and 7.0–22.9°C in later embryonic stages (neural keel to hatching). The lower TL50 for production of swim-up larvae was 9.8°C. Newly hatched yellow perch larvae tolerated a temperature range of 3–28°C for 24 h when incubated and hatched at 18°C (Environmental Research Laboratory-Duluth, unpublished data); however, larvae were inactive at 5.3°C. Optimum yields of swim-up larvae were produced when initiated incubation temperatures (4.9–10.0°C) were increased 1 deg. C/day (range 4.9–24.3°C). Rising temperature regimes also favored shorter hatching periods and lower incidence of abnormalities than did constant temperatures. In pikeperch, rising temperature regimes favored shorter hatching periods and lower incidence of abnormalities (Muntyan 1975) than did constant incubation temperatures (Muntyan 1967). Optimum temperatures for development of pikeperch increased from 12 to 20°C for spawning, 14 to 23°C for larvae (1–7 days old),

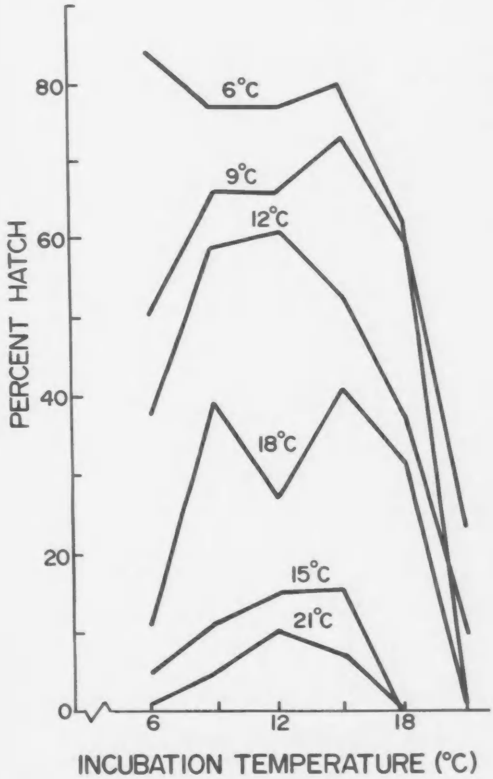

FIG. 3. Percentage of walleye (*Stizostedion vitreum vitreum*) eggs that hatched at various incubation temperatures after fertilization at six temperatures from 6 to 21°C (from Smith and Koenst 1975).

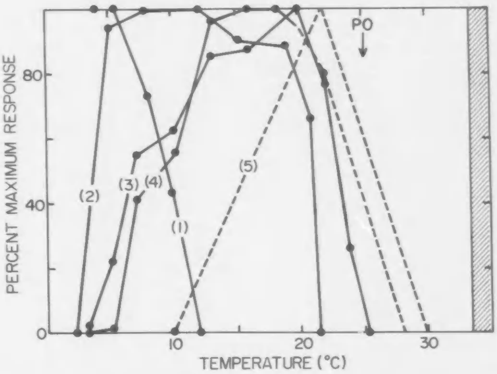

FIG. 4. Temperature limits for survival of different stages in the life cycle of yellow perch expressed as percentages of maximal responses. (1) Maximal percentages of females spawning after exposure to various chill temperatures. (2) Egg survival from fertilization to formation of the neural keel (C. F. Kleiner, U.S. EPA, Monticello, Minn., personal communication). (3) Egg survival from neural keel formation to hatch. (4) Larval survival from hatch to swim-up stage. (5) Predicted survival of feeding larvae on excess rations based on larval rearing observations. Arrow designates physiological optimum (PO) of juveniles and shaded area the zone of thermal resistance, where survival is time-dependent, bounded on the left by the ultimate upper incipient lethal temperature, for juveniles.

and 14 to 26°C for larvae (22–35 days old) (Zhdanova 1966). The upper lethal temperature for larvae (4.5–5.8 mm long) was 30–32°C, and the lower lethal limit was 6.0–6.5°C. A drop in water temperature below 10°C was not considered desirable for larvae (Woynarovich 1963; Zhdanova 1966). Temperature fluctuations within normal tolerance limits of walleye embryos were not considered harmful (Allbaugh and Manz 1964).

The range of observed spawning temperatures in the percids reviewed corresponds closely with embryo tolerance limits (Table 2): the TL50 limits are lowest in the walleye (<6.0–19.2°C), highest in pikeperch (9–24°C), and intermediate in sauger and the two perches (6.0–21°C). Similar trends were also observed for extreme spawning temperatures. Where field observations were most extensive, as in perch, the maximum spawning temperature corresponded closely to the upper TL50 for embryos. The lowest spawning temperature observed for each species, however, was 2–4 deg C lower than the lower TL50 limit for embryos. A closer correspondence may exist between the lowest spawning temperature and temperature tolerance of early embryonic phases, as for yellow perch (3.7°C). In contrast, temperate stenotherms are adapted to temperatures below 15°C for spawning and embryo development; and temperate eurytherms to temperatures between 15 and 32°C (Table 3).

Temperatures required to initiate feeding among percid larvae appear to be higher than those required by embryos. No perch and ruffe larvae survived Kammerer's (1907) feeding trials at 10°C; however, he had some survive at higher temperatures. Hubbs (1971) observed that three of seven samples of larval yellow perch fed at 12.5°C, as did one of nine samples at 9.5°C. Smith and Koenst (1975), who reared larval sauger and walleye to 40 mm, reported that, for each species, only 1% survived at 18°C and 8% at 21°C; none survived at 15°C or less. Similar results were observed by Olson (1974). Hale and Carlson (1972), who reared yellow perch larvae at 20–21°C, obtained a mean survival of 63%

TABLE 3. Temperature requirements of some fish species associated with percids.

Species	Reproduction range (C)[a]	Physiological optimum (C)[b]		Lethal temp (°C)[c]	
Brook trout	1.6–12.7[d,e]	15.6[s]	(L)	20.1[s]	(L)
	0.3–10[f]	16.1[e]	(A)	25.3[z]	(J)
Rainbow trout	3–15[g]	17.2[t]	(J)	25.0–26.5[t,aa,bb]	(J)
	0.3–15[f]			21[cc]	(A)
Lake herring	1.2–9.1[h]	18.1[u]	(L)	19.8[u]	(L)
	1.1–5.0[i]			26.2[dd]	(J)
White sucker	8.1–21.2[j]	26.9[j]	(L)	30.5[j]	(L)
	6.1–23.3[k]			29.3–31.2[ee,ff]	(J)
Northern pike	6.9–19.2[l]	26[l]	(L)	28.4[l]	(L)
	3–18.5[l]			33[gg]	(J)
				29.0[hh]	(A)
Largemouth bass	11.6–27.9[m]	30.0[v]	(L)	36.4[ii]	(J)
	15.6–26.7[f]				
Bluegill	21.9–33.8[n]	30.1[w]	(J)	37.3[n]	(J)
	17.2–32.3[f]	32.3[x]	(J)		
Trench	16.5–32.2[o]			33.8[jj]	(J)
	14–27.5[o]			39.3[kk]	(J)
Carp	12.5–30.0[p]	32.0[y]	(J)	35.7[ll]	(J)
	16–26[q,r]			40.9[kk]	(J)

[a] Spawning temperature range observed in the field (upper value); lower and upper TL50s of eggs incubated at constant temperatures from fertilization to hatch in the laboratory (lower value).

[b] Physiological optimum based on growth data. Higher value for bluegill and value for carp are final preferenda in laboratory. L, larvae; J, juvenile; or A, adults.

[c] Ultimate upper incipient lethal temperature. Higher values for tench and carp are critical thermal maxima. L, larvae; J, juvenile; or A, adults.

[d] Embody (1934); [e]Hokanson et al. (1973b); [f]Hokanson and Biesinger (1977); [g]Kwain (1975); [h]Colby and Brooke (1970); [i]Carlander (1969); [j]McCormick et al. (1977); [k]Trautman (1957); [l]Hokanson et al. (1973a); [m]Kelly (1968); [n]Banner and Van Arman (1973); [o]Reznichenko et al. (1968); [p]Keiz (1959); [q]Swee and McCrimmon (1966); [r]Sigler (1958); [s]McCormick et al. (1972); [t]Hokanson et al. (1977); [u]McCormick et al. (1971); [v]Strawn (1961); [w]Lemke (1977); [x]Ferguson (1958); [y]Pitt et al. (1956); [z]Fry et al. (1946); [aa]Alabaster and Welcomme (1962); [bb]Bidgood and Berst (1969); [cc]Coutant (1970); [dd]Edsall and Colby (1970); [ee]Brett (1944); [ff]Hart (1947); [gg]Scott (1964); [hh]W. B. Horning II, U.S.EPA, Newton, Ohio, personal communication; [ii]Hart (1952); [jj]Alabaster and Downing (1966); [kk]Horoszewicz (1973); [ll]Black (1953).

after 3 wk. Kudrinskaya (1970b) determined that ration size had a pronounced effect on growth and survival of perch and pikeperch larvae at 19.3°C, but had less effect at 16.0°C. These observations suggest that feeding and survival of well-fed percid larvae is possible above 10°C and optimal above 20°C. Temperature optima for survival would be lower if rations were restricted. The temperature requirement of yellow perch larvae deduced from these feeding trials is illustrated in Fig. 4.

Studies on the effects of temperature and ration size over the biokinetic range of percid larvae are needed for a fundamental understanding of the critical period of survival. Temperature requirements of feeding percid larvae are poorly known; high mortality of larvae occur when sufficient quantities of preferred food organisms are lacking (Menshutkin et al. 1968; Kudrinskaya 1970a; Hale and Carlson 1972). Larval percids have similar specific food requirements at the start of feeding — principally copepod nauplii, the large rotifer *Polyarthra*, and small cladocerans, such as *Bosmina* and *Chydorus* (Woynarovich 1960; Deelder and Willemsen 1964; Menshutkin et al. 1968; Siefert 1972). Many factors other than temperature and food density tend to reduce survival of percid larvae — such as high light intensity, high larval density (resulting in cannibalism), and transfer methods between aquaria (Woynarovich 1960; Hale and Carlson 1972; Olson 1974).

Embryonic and larval development rate — The median times required for percids to reach various stages of embryonic and larval development decrease exponentially with increasing temperature. Hokanson and Kleiner (1974) described the median times required to reach various morphological stages and physiological events in yellow perch embryos and larvae at various constant temperatures (Fig. 5). Median time to hatch ranged from 6 days at 19.7°C to 51 days at 5.4°C. Little difference was found in time to mass hatch at a given temperature among yellow perch (Hokanson and Kleiner 1974), Eurasian perch (Swift 1965; Kokurewicz 1969), pikeperch (Deelder and Willemsen 1964; Kokurewicz 1969; Muntyan 1975), and walleye and sauger (Smith and Koenst 1975), except that pikeperch developed at higher temperatures. Both perches and the pikeperch tended to hatch prematurely at low incubation temperatures where survival was low.

High temperatures can shorten the time for feeding opportunities of newly hatched larvae. The median period between swim-up and death of unfed yellow perch larvae was 9 days at 19.8°C and 21 days at 10.5°C (Hokanson and Kleiner 1974). Feeding trials at higher temperatures suggested that feeding started when the larvae became free-swimming. The critical period when survival-dependent feeding of larval perch must start is even shorter than the aforementioned intervals, since death of unfed larval fishes occurs when offered food after a certain degree of emaciation is reached (Toetz 1966). Woynarovich (1960) reported that pikeperch larvae were unable to withstand starvation for ½ day at the start of feeding, whereas larvae 8–10 days old could survive as long as 2 days without food. Studies by Priegel (1970) indicated that walleye larvae in the Wolf River, Wisconsin, starved to death unless they reached a lake environment where plankton production was high within 3–5 days after hatching. In larval perch that received no food during the first 7 days after hatching and were then allowed to feed for 20 days, mortality was 94% in aquaria and 66% in a pond (Menshutkin et al. 1968). All larvae starved for 9 days after hatching died when placed in the pond or aquaria. In summary, the importance of timing of larval development with production of specific food organisms is evident.

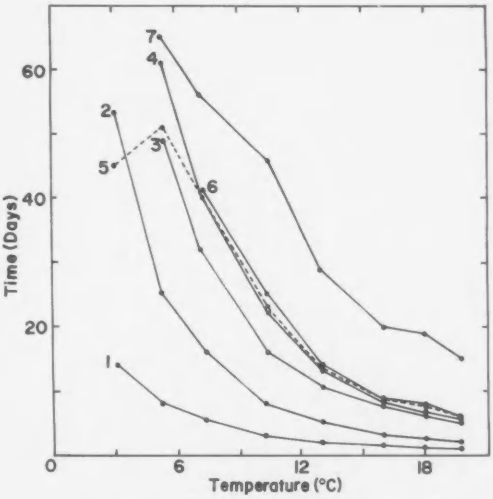

FIG. 5. Median times for development to various stages of yellow perch embryos and larvae at various temperatures. 1, Neural keel; 2, heart beat; 3, retinal pigmentation; 4, branchial respiration; 5, mass hatch; 6, swim-up larvae; 7, mortality of unfed larvae (from Hokanson and Kleiner 1974).

Year-class strength — Reproduction of *Perca* and *Stizostedion* spp. depends on a rising temperature regimen for optimal recruitment, given other favorable conditions. Busch et al. (1975) observed a high positive correlation between walleye year-class strength and rate and regularity of water-temperature rise on the spawning grounds during the spawning and incubation periods. Strong year-classes of perch (Kipling 1976) and pikeperch (Nagięć 1977) developed when the water is warm during periods of reproduction, though suitable temperatures do not always produce strong year-classes. Water temperature has not always been implicated as the sole factor influencing recruitment of percids. Willemsen (1977) and Clady (1976) concluded that a sequence of favorable factors probably determines the success of a year-class and that no one factor can be considered as a decisive cause for fluctuations in year-class strength.

Growth

Bioenergetics and growth — Growth can be viewed as the net effect of the environment on the relation between food consumption, metabolism, and activities of an organism. Warren (1971) discussed these theoretical relationships and the fate of consumed food in terms of a bioenergetic budget (Fig. 6). Temperature influences food-consumption rate of a fixed ration and distribution of assimilated energy into different

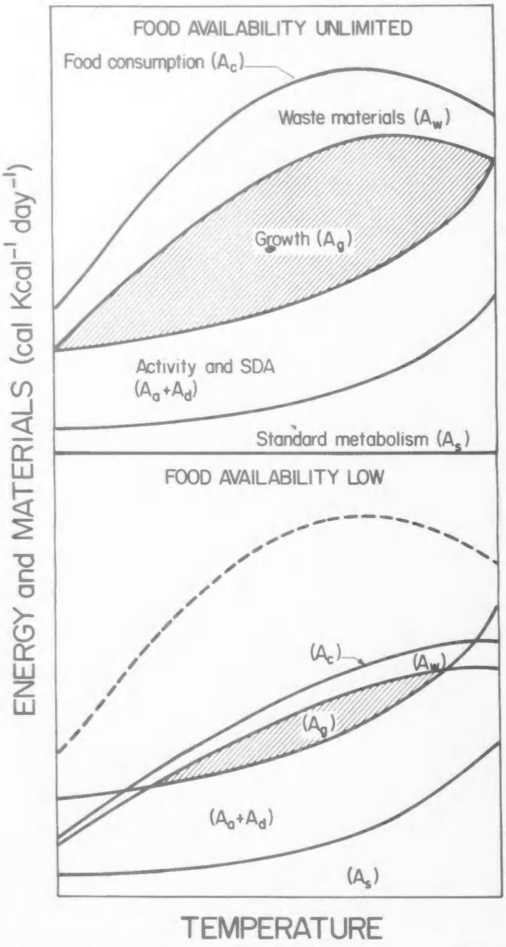

FIG. 6. Theoretical effects of temperature change on the food consumption, energy budget, and scope for growth of a hypothetical poikilothermic animal having food available in different amounts (from Warren 1971).

components such as metabolism, activity, and growth of the organism.

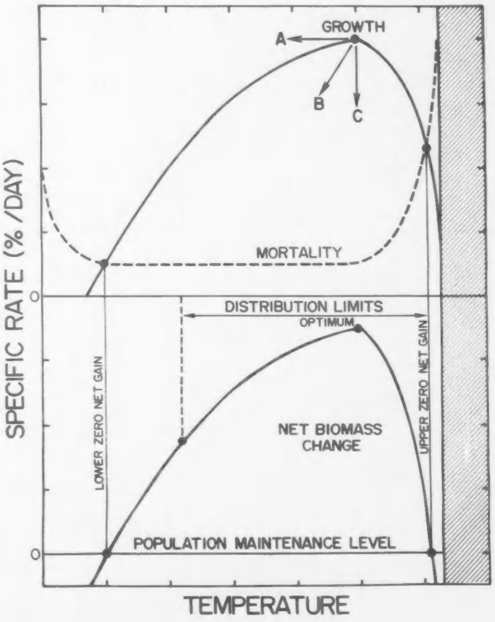

FIG. 7. Constant temperature effects on specific rates of growth (g), mortality (i), and net biomass change ($k = g - i$) for a hypothetical fish species fed excess rations. The zone of thermal resistance, where survival is time-dependent, is represented by the shaded area, bounded on the left margin by the ultimate upper incipient lethal temperature. Graphical endpoints that have particular physiological and ecological significance are identified by circles and labeled in the lower panel. Predicted shifts in growth response and optimum endpoints attributed to different stimuli illustrated in upper panel: A, diel fluctuation of acclimatization temperature of *Salmo gairdneri* (Hokanson et al. 1977); B, restricted food rations of *Oncorhynchus nerka* (Brett et al. 1969); C, increased initial size of *O. nerka* (Shelbourn et al. 1973).

Several factors besides temperature should be taken into account when one compares growth studies conducted under different experimental conditions or analyzes population differences. The proportion of assimilated energy available for growth increases with temperature to a peak, and then declines as temperature increases further (Fig. 7). For small fish fed unlimited rations, the optimum temperature is skewed toward the upper biokinetic range, only a few degrees below the upper lethal temperature. Deviations from this pattern of growth are influenced by several variables as illustrated in Fig. 7. Diel temperature fluctuations (A) shifted the growth response of *Salmo gairdneri* horizontally towards a lower mean equivalent constant temperature in direct proportion to the amplitude of the cycle (Hokanson et al. 1977). Temperature fluctuations enhance growth in relation to corresponding mean constant temperature levels below the optimum, and retard growth at higher temperatures. Restricted rations (B) can reduce the scope for growth and optimum temperatures of *Oncorhynchus nerka* (Brett et al. 1969). Increased size (C) can also decrease growth rate of *O. nerka* at all temperatures which produces a less pro-

TABLE 4. Some optimum temperatures for various percids.

Species	Growth optimum		Temp preference[a] (°C)		Physiological optimum (°C)
	Initial size or age	Temp (°C)			
Sauger	9.6 cm	22.0[c]	18.6–19.2 (lake)	(F)[h]	22.0
			22–28 (stream)	(F)[i]	
Walleye	8.5 cm	22.1[c]	20.6–23.2	(F)[h]	22.6
	6.5 cm	25.2[c]	21	(F)[j]	
Yellow perch	5.2–23.7 g	23[d]	20.0–29.0	(L)[k,l,m]	24.7
	(Fall–spring study)		19.7–27.1	(F)[h,n]	
	0.5 g (Summer)	28[e]			
Eurasian perch	2 yr (15–16 cm)	26[f]	18–27.3	(F)[o,p]	25.4
	Larvae	25–30[g]			
Ruffe	Larvae	25–30[g]			
Pikeperch	1 yr	28–30[f]	29	(L)[f]	27.3
	13 cm		24	(F)[q]	

[a] Laboratory (L) final preferendum based usually on juvenile fish; field distribution values (F) usually based on adults.

[b] Average of reported growth optima and temperature preferences of a given species.

[c] Smith and Koenst (1975); [d] Schneider (1973); [e] McCormick (1976); [f] Willemsen, personal communication; [g] Kammerer (1907); [h] Ferguson (1958); [i] Gammon (1971); [j] Johnson (1969); [k] McCauley and Read (1973); [l] Barans and Tubb (1973); [m] McCauley (1977); [n] Neill and Magnuson (1974); [o] Neuman (1974); [p] Horoszewicz (1973); [q] Deelder and Willemsen (1964).

nounced optimum temperature (Shelbourn et al. 1973). Growth rates of young walleye and yellow perch were faster for 16-h days than for 8-h days at both 16 and 22°C (Huh et al. 1976). Growth of young walleye appeared to be temperature dependent, whereas that of yellow perch was more photoperiod dependent. Inadequate food type can also increase maintenance requirements and reduce growth rate of yellow perch at the higher temperatures (Schneider 1973).

Optimum growth temperatures for six percids ranged from 22 to 28°C (Table 4); they were lowest in walleye and sauger, intermediate in the two perches and the ruffe, and highest in the pikeperch. Variation in growth optima within species reflects differences in age, diet, and season of test. Large differences between treatment intervals also decrease the accuracy of the reported optimum value among tests. In contrast, the growth optima ranged from 15 to 18°C for three temperate stenotherms, from 26 to 27°C for two other temperate mesotherms, and from 30 to 32°C for four temperate eurytherms (Table 3).

Annual growth — Annual growth increments are a function of the size of fish and they accumulate daily increments of growth that vary with the available food supply and temperature over the year. Food supplies are known to vary seasonally and thus would tend to destroy any long-term correlation with temperature. Food-consumption rate of a walleye population in Lake of the Woods, Minnesota, was 1% of body weight during June, 2% during July, and 3% during August and September (Swenson and Smith 1973). Food consumption of adult perch in Loch Leven, Scotland, decreased from 6.5 and 6.7% of their body weights in June and July, respectively, to 3.2% in September (Thorpe 1974). Energy content of food items is also variable and may be seasonal (Kelso 1973). If one truly wants to understand how temperature influences annual growth, one must reexamine seasonal growth relationships of populations in the context of bioenergetics, which will require frequent monitoring of environmental conditions prevailing during the entire year.

Descriptions of annual increments of growth provide limited information of the effects of the environment on seasonal growth (Warren 1971). Low correlation between annual growth increments and mean water temperature does not imply that temperature has no effect, since temperature is known to exert a continuous influence on the food consumption and fate of assimilated energy. Low correlation may result from lack of accurate environmental information including fish-acclimatization temperature, prey and predator biomass, high population density (which restricts food rations), seasonal variations in food supply, and use of inappropriate statistical models of growth due to lack of sound experimental data. Coble (1966) found a high correlation between annual growth increment of yellow perch and mean water temperature (14.5–16.0°C) from June to October in South Bay, Lake Huron. Such temperatures are considerably below the optimum or preferred temperatures of yellow perch, suggesting that temperature was controlling growth in this environment even when rations available to fish were restricted. LeCren (1958) found a high correlation between annual growth and degree-days above 14°C over a 22-yr period in an exploited population of Eurasian perch in Lake Windermere, England. Growth rate of this population improved in response to exploitation, suggesting that food was limiting growth in the unexploited population.

Survival

Lethal temperatures — The lethal temperatures of percids are variable because they provide the mechanism to resist temperature extremes during seasonal changes. Fry (1947) provided several useful definitions in measurement of the lethal factor. The lethal temperatures of fish have been determined by either the incipient lethal temperature or the critical thermal maximum (CTM) method. In tests in which temperature was increased 6°C/h, the CTM was about 3.5°C higher than the respective incipient lethal temperature (Horoszewicz 1973). The CTM method is commonly used by Eurasian authors, whereas the incipient lethal temperature test is commonly used by North American authors.

Any factor that influences thermal acclimation or the effective time influences the apparent lethal temperature. When an organism is transferred from one water temperature to another, thermal acclimation takes place within hours for increasing temperatures, but is not completed for several days for decreasing temperatures (Brett 1944). Fish acclimated to diel temperature fluctuations compensate for high and low temperatures simultaneously and have an increased range of temperature tolerance (Feldmeth et al. 1974). Pupfish, *Cyprinodon nevadensis amargosae*, acclimated to a diel temperature cycle from 15 to 35°C had critical thermal maxima equal to those acclimated to constant 35°C and had critical thermal minima equal to those acclimated to constant 25°C (the mean of the cycle). The critical thermal minimum, which reached its lowest point after 22 days of acclimation, was changed more slowly than the maximum, which was reached in <7 days. Hart (1952) observed seasonal differences in thermal tolerance of several species; however, some of these differences were due to incomplete acclimation in winter studies, which was attributed to inadequate acclimation time or inadequate feed in stock tanks. Seasonal changes in day length may contribute to these differences in thermal responsiveness (Fry 1957). Brett (1944) observed no effect of starvation for 40 days on the upper incipient lethal temperature of *Ameiurus nebulosus* in summer tests. Low dissolved oxygen concentrations can block thermal acclimation and normal seasonal response to temperature (Brett 1946).

Juveniles are perhaps the most thermally tolerant phase in the life cycle of percids. For example, the ultimate upper incipient lethal temperature of juvenile and adult yellow perch varied from 29.2 to more than 33° C for various test conditions (Table 5), but the 24-h TL50 for newly hatched larvae was 28° C, as previously described. Other examples are sparse among percids, but examples are listed for cohabitant species in Table 3. Weatherley (1963b) and Horoszewicz (1973) concluded that size did not influence lethal temperatures among juvenile fish; however, Bailey (1955) observed that adults died and only juveniles survived high temperatures in a Michigan pond.

In juvenile percids, the ultimate upper incipient lethal temperatures generally fell in the range between 29.2 and 35.0°C for various species and test conditions (Table 5). Since tests were seldom conducted under closely similar conditions, the conditions for acclimation (laboratory) or acclimatization (field), age, season, and test duration or rate of temperature rise are reported so that the experimental variation may be noted. Thermal tolerance appears to be lowest in the walleye and sauger, and highest in pikeperch. The upper incipient lethal temperature of yellow perch alone varied from 29.2 to more than 33°C, depending on test conditions. The highest values of the ultimate upper incipient lethal temperature occurred for summer tests at the highest acclimation temperatures, increasing slowly to test temperatures. Under comparable conditions the two perches had almost identical thermal tolerance limits. The ruffe had a relatively low upper incipient lethal temperature of 30.4°C; however, the acclimation temperature (20°C) was the lowest in this series. The critical thermal maximum for ruffe was similar to that for both perches considering differences in acclimation and rate of temperature increase. In contrast, the ultimate upper incipient lethal temperature of juvenile cohabitants ranged from 25.0 to 26.5°C for three temperate stenotherms, from 29 to 33°C for two other temperate mesotherms, and from 34 to 37°C for four temperate eurytherms (Table 3).

TABLE 5. Lethal temperatures for various percids.

Species	Acclimation temp (°C)	Life stage[a]	Season[b]	Ultimate upper incipient lethal temp[c] (°C)	Critical thermal max[d] (°C)
Walleye	25.8 (2 wk) 3–4°C/h to test temp	J — 11.5 cm	F	31.6[e] (96)	
Sauger	25.8 (2 wk)	J — 11.9 cm	F	30.4[e] (96)	
Yellow perch	23–25 (field)	A — 12.5 cm	Su	30.9[f] (12)	
	22–24 (field)	J, A — 2.9 to 50 g	Su	29.2[g] (24)	
	25 (4 days)		Su	32.3[h] (13)	
	25 (20 days)	J — 6 to 24 g	W	29.7[i] (83)	33.4[i] (1)
	28 (1°C/day to test temp)	J — 0.5 g	Su	33–34[j] (24)	
Eurasian perch	25 (24 days)	J — 8.4 cm	S	31.4[k] (16.7)	
	30 (0.5°C/day)	J — (2 yr)		33.5[l] (24)	
	27.3 (field)	J	Su	32[m] (<100)	35.9[m] (6)
	30 (7 days)	J — 0.9 to 2.2 g	Su		35.5[n] (4)
Ruffe	20 (11 days)	J — 8.6 cm	F	30.4[k] (16.7)	
	24.1–25.7 (field)	J — 2.8 to 6.2 cm	Su		34.5[m] (6.0 to 7.2)
Pikeperch	25.6 (field)	J — 3.6 to 9.3 cm	Su	34.3[m] (16.7)	37.0[m] (6.0 to 7.2)
	30 (0.5°C/day to test temp)	J — (1 yr)	W	35.0[l] (24)	

[a] A, adult; J, juvenile; total length in centimetres; wet weight in grams.
[b] F, fall; W, winter; S, spring; Su, summer.
[c] Effective time in hours in parentheses. Fish exposed to sudden temperature increases except where noted.
[d] Rate of temperature increase (°C/h) in parentheses.
[e] Smith and Koenst (1975); [f] Brett (1944); [g] Black (1953); [h] Hart (1952); [i] Hart (1947); [j] McCormick (1976); [k] Alabaster and Downing (1966); [l] Willemsen, personal communication; [m] Horoszewicz (1973); [n] Weatherley (1963b).

The lethal temperatures were generally 6–10°C higher than the growth optima among cold-water species, but only 3–6°C higher than the growth optima among warm water species. Optimal performance near lethal temperatures allows a wider thermal range for activity and scope for growth among the warmwater species.

Annual survival — The effects of food, fish size, and temperature regimes are important to understanding seasonal mortality among fish populations. Several authors have reported increased mortality in growth experiments at supraoptimal temperatures below the incipient lethal level (Strawn 1961; Smith and Koenst 1975; Brett et al. 1969). Food can act as an accessory factor contributing to increased mortality among fish reared at elevated temperatures (Fig. 7). A 96-h TL50 corresponds with a specific mortality rate of 17.3%/day. In the biokinetic range for growth below the optimum temperature, specific mortality rate declined to a low constant rate <0.5%/day among larval and young fishes (Hokanson et al. 1973a; McCormick 1976;

Hokanson et al. 1977). Within these normal temperature ranges, other factors such as food (Dobie 1969; Alm 1954; Forney 1974) and cannibalism or predation (Alm 1951; Sumari 1971) can limit survival.

Low winter temperatures can also contribute to increased mortality in fish populations (Fig. 7). Juvenile and older percids are considered able to survive temperatures near freezing (Hart 1947), but exposure periods for lower incipient lethal temperature tests are usually <1 wk. Some evidence suggests that in northern habitats fish must reach a certain size to survive their first winter. Survival of percid larvae is poor below 10°C, as noted previously. Yearling walleye, like the young of other species, were rather sparse in Canada's northern waters (Regier et al. 1969). Forney (1966) observed that population mean lengths of young-of-the-year walleye from Oneida Lake, New York, increased between fall and the following spring and attributed the size increase to selective mortality among smaller fish rather than to growth during the winter. Svardson and Molin (1973) correlated year-class strength of pikeperch with summer temperatures; the higher summer temperatures promoted growth, and ultimately overwinter survival. A strong selective mortality of females occurred among stunted populations of yellow perch in some Laurentian lakes of Canada (Newsome and LeDuc 1975). The mature female, because of lack of food in summer, could not build sufficiently large fat reserves to maintain normal body and maturation functions throughout the winter. Bacterial infections and mortality in fish populations were most intense in the spring, as the water temperature increased, and were lowest in summer, when antibody production was high (Bisset 1948). Acquired antibody titer was reduced and antibody production was nil at winter temperatures.

Net biomass change — Knowledge of the seasonal course of fish growth and mortality helps explain the magnitude of biomass at a given time and may provide insight into factors affecting production and yield. The specific rate of net biomass change (k) is equal to the specific growth rate (g) minus the specific mortality rate (i) (after Ricker 1958); the relationship between these parameters is illustrated in Fig. 7. The "population maintenance level" is equivalent to the initial weight of the population or the weight over some time interval whenever the specific growth and mortality rates are equal. The graphic endpoints that intersect the population maintenance level describe the lower and upper zero net gain limits for those test conditions. These graphical endpoints provide additional reference points to correlate with distribution limits of a species. These statistics are not readily available in the literature because mortality frequently has not been reported in growth studies, or tests have been conducted over only a narrow temperature range. McCormick (1976) provided a complete description of specific growth and mortality rates over the biokinetic range of juvenile yellow perch fed excess rations. If the abnormal perch at 32°C are considered as deaths, then the lower and upper zero net biomass gain limits were 6 and 31°C, respectively, and the growth optimum for excess rations was 28°C. The upper zero net biomass gain for juvenile walleye was 29°C, as graphically extrapolated from the data of Smith and Koenst (1975). This model of population growth accounts for maximum rate of biomass increase at temperatures near optimum for a given food ration. Supraoptimal temperatures produce a small biomass consisting of a few large individuals, and suboptimal temperatures produce large numbers of smaller individuals (Hokanson et al. 1977). This model also accounts for reduction in population biomass and negative production at temperatures outside the limits of zero net biomass gain, as has been reported during the winter in natural populations (Chapman 1967; Kelso and Ward 1972).

Activity

Preferred temperature — Multiple directive stimuli influence fish activity and contribute towards large variations in preferred temperatures of percids. Fry (1947) provided several useful definitions of activity and preferred temperature relations among fishes. Observations of percids temperature preference in laboratory and field studies varied from 18 to 29°C (Table 4). The variation from 19.7 to 29.0°C in yellow perch alone obscures differences among species. Yellow perch are difficult to condition to the gradient tank and are imprecise in their thermal preference. McCauley and Read (1973) reported a mean final preferendum for yearling yellow perch in summer of 23.3°C with SD = ±2.5°C. This value indicates that 99% of the observations of temperature selection (i.e. mean ±3 SD) fell in a range from 15.8 to 30.8°C in their study. Yellow perch continue to invade temperatures in excess of their upper incipient lethal temperature and die, especially when acclimated to low temperatures (Ferguson 1958; Barans and Tubb 1973).

Acclimation temperature is a principal factor influencing temperature preference (Fry 1947). At low acclimation temperature fish have a strong tendency to move into warm water such as thermal plumes or the epilimnion. At acclimation temperatures above the final preferendum, fish tend to seek cooler water refugia such as the hypolimnion or groundwater springs. Barans and Tubb (1973) reported that preferred temperatures of young yellow perch varied from 13 to 29°C when ambient Lake Erie temperatures varied from 1 to 24°C, respectively, and no final preferendum was measured.

Young fish generally selected higher temperatures than adults in all seasons. The high preferred temperature of 29°C observed for young-of-the-year yellow perch in summer by Barans and Tubb (1973) corresponds closely to the growth optimum (28°C) reported for similar-aged fish in another summer test (McCormick 1976). McCauley and Read (1973) observed that juvenile yellow perch selected temperatures 3°C higher than adults when acclimated to 24°C during fall. McCauley (1977) found no marked seasonal difference in temperature preference of adult yellow perch at a given acclimation temperature, but found that temperature preference in winter of yellow perch acclimated at 5°C was 13°C, and thus higher than the safe limit for maturation (<10°C). Acclimation of adults to constant temperatures for periods up to 1 yr affects gonad maturation and resorption and perhaps influences the normal thermal responsiveness of the species.

Studies on the relation of temperature to tolerance, preference, metabolic rate, performance, circulation, and growth all point to a common physiological optimum for a given species (Brett 1971). Therefore, growth optima and preferred temperatures were averaged to derive an estimate of the physiological optimum for a species. The physiological optima varied from 22°C for walleye and sauger, 25°C for Eurasian and yellow perch, to 27°C for pikeperch (Table 4). In contrast, the physiological optima varied from 15 to 18°C for three temperate stenotherms, from 26 to 27°C for two other temperate mesotherms, and from 30 to 32°C for four temperate eurytherms (Table 3).

Field distribution — Catch per unit effort of a species along a habitat gradient, expressed as a range or median temperature, provides useful information on a species' field distribution. Dendy (1948) concluded that accurate predictions of fish-depth distribution could be made on the basis of the thermal profile of a stratified waterbody if allowance was made for unfavorable oxygen concentrations. He found sauger at a greater depth and lower temperature stratum (18.6–19.2°C) than walleye (20.6–23.2°C) in Tennessee reservoirs. Swenson and Smith (1976) made similar observations in Lake of the Woods, Minnesota. Laboratory and field temperature preferences of *Perca* spp. covered a similar intermediate range (18–29°C) among percids (Table 4). Pikeperch apparently have the highest preferred temperatures (24–29°C) among percids. The range of values for field distribution reported in Table 4 reflects a restricted distribution where higher or lower temperatures were available in their respective habitats. Stream populations may have higher field-distribution limits because depth or light are not covariates with temperature along a horizontal gradient. Hile and Juday (1941) recognized that the bathymetric distribution of certain species and age-groups was not always correlated with temperature and oxygen in various lakes and that local conditions go far towards obscuring their influence. Therefore, a more critical evaluation of other directive factors that influence diel and seasonal migrations of percids follows.

Day length and light intensity can influence the diel activity cycle and acclimatization temperature of a fish. Walleye (Carlander and Cleary 1949; Niemuth et al. 1972), sauger (Nelson 1968), and pikeperch (Deelder and Willemsen 1964) are reported to have nocturnal behavior patterns and thrive in turbid waters, whereas ruffe (Kammerer 1907), yellow perch (Hasler and Bardach 1949; Scott 1955), and the Eurasian perch (Eriksson 1974) are diurnal species. Larval yellow perch were most abundant in surface waters at night, whereas older fish were inactive, resting on the bottom (Ward and Robinson 1974). Yellow perch spawned at night in shallow water (Scott and Crossman 1973). Adult sauger had a nocturnal activity cycle in a shallow experimental stream channel with a horizontal temperature gradient (Fig. 8). The sauger were active in the warmwater zone at night, and rested in the open cool-water zone by day. Sauger A experienced a daily mean temperature of 10.4°C (range 7.0–13.0°C) and traveled 1097 m, while sauger B experienced a daily mean temperature of 6.8°C (range 5.3–11.4°C) and traveled 2804 m. In the absence of a heated gradient when the channels were covered by ice and snow, sauger were diurnal. Daytime activity of walleye and sauger in shallow water was increased by approach of a storm, low light intensity, wind action on shallow reefs, and turbid water (Eschmeyer 1950; Arnold 1960; Scott and Crossman 1973; Scherer 1976). Sauger generally thrive in a more turbid water habitat than walleye (Scott and Crossman 1973), which may account for a deeper bathymetric distribution of sauger in the same habitat.

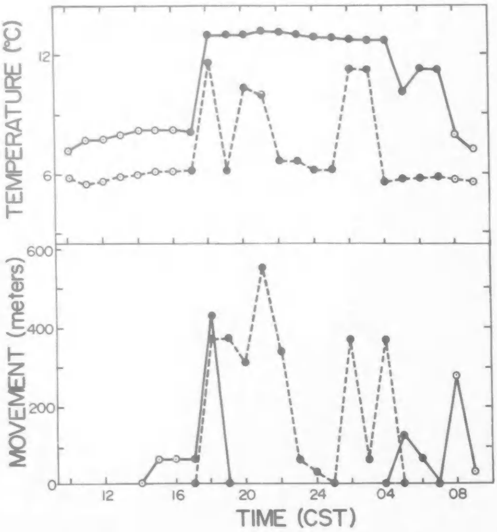

FIG. 8. Diel movements and acclimatization temperatures of two adult sauger (*S. canadense*) in a thermal gradient (5.3–13.4°C) in an outdoor experimental stream channel (518 m long) on January 6–7, 1975, as determined from tagging with ultrasonic transmitters. ———, sauger A; – – – – – –, sauger B; ○, daylight; ●, darkness (Environmental Research Laboratory–Duluth, unpublished data).

Food distribution and abundance can act as directive factors influencing fish distribution and activity. Swenson and Smith (1973) observed that walleye feeding in summer was uniformly distributed throughout the day and night during periods of low food consumption. When food consumption increased, feeding activity was greater at night and during early morning hours. In Lac la Ronge, Saskatchewan, walleye followed their cold-water prey, *Coregonus artedii*, offshore into deeper water in summer, even though the open waters were cooler than their temperature preference (Rawson 1957). In midlatitude waters walleye fed on prey such as yellow perch and benthic invertebrates found within their preferred temperature range (Dobie 1966). *Coregonus artedii* were not used as food in these waters except in cooler seasons when they were near shore. In a southern California reservoir walleye fed almost exclusively on warmwater prey such as *Dorosoma petenense* and were found in the warm surface waters at night (Miller 1967). Diel movements of pikeperch larvae corresponded closely to those of their prey (Kudrinskaya 1970a). Larvae followed copepods out to the warmer river channel, where larval concentration increased 40-fold in surface waters at night and only 4-fold in bottom layers; in contrast, the larvae were 15–20 times more abundant in bottom than in upper layers during daylight. Food availability increases the proportion of time fish spend at a nonpreferred temperature (Neill and Magnuson 1974). Inferences of thermal history or acclimatization temperature based on catch data from one portion of a day may be of relatively little value.

Age also plays an important role in the seasonal migration and temperature history of fish stocks. Ferguson (1958) noted that final preferenda of young fish in laboratory tests were higher than thermal limits for distribution of adults in field observations. Hile and Juday (1941) described an exception to this depth distribution, whereby small yellow perch were found at greater depths than larger ones. Tagging studies of walleye stocks suggested that the shallow, western basin of Lake Erie was a milling or mixing area for juveniles, whereas southern Lake Huron and the north shore of central and eastern Lake Erie were occupied mainly by adults (Ferguson and Derksen 1971). All percid larvae have a pelagic existence in offshore areas and migrate to the littoral area by late summer (Faber 1967; Priegel 1969; Kudrinskaya 1970a; Kuznetsov 1970; Spykerman 1974; Ward and Robinson 1974). The shoreward migrations of young percids are coincident with changes in food preferences from zooplankton to littoral forms such as benthic invertebrates and fish.

The maturation cycle and physiological condition of adult percids is important in governing seasonal migrations of fish stocks. The Eurasian perch showed a well-marked seasonal migration in Lake Windermere, England, living in the top 10 m in summer and at depths between 18 and 27 m in winter (Allen 1935). Perch migrate to the deeper waters in October and November and towards shore in April, when lake temperatures normally rise. This migration to deeper water in fall is coincident with gonadal development, as discussed previously. Allen argued that shoreward migrations are related to ripening of gonads since spawning takes place shortly thereafter. Furthermore, temperatures at the greater depths at which perch spend the winter do not increase much even by summer, whereas surface water temperatures increase to temperatures preferred for spawning. Similar seasonal migrations have been observed in yellow perch (Ferguson 1958; Brazo 1973) and walleye (Forney 1966; Johnson 1969). This seasonal migration of adult percids to deeper water in fall and winter and shoreward in the spring has not been described by laboratory studies of preferred temperatures.

Multiple stimuli may direct percids offshore by fall to bring them into conditions favorable for gonad maturation. Offshore migrations begin in summer as surface water temperatures increase and the thermocline depth increases. Percids seek the deeper waters which remain warmer than the shoals in late fall and early winter. Eriksson (1974) observed the diel and annual rhythm of activity and vertical distribution of Eurasian perch in a large laboratory tank. During winter perch were less active and stayed near the bottom of the tank. During summer they were about as numerous in the upper part of the tank as in the lower. Thermal plumes to the upper Mississippi River did not attract yellow perch in winter, but spawning aggregations frequented the area in spring (M. J. Ross, University of Minnesota, Minneapolis, Minn., personal communication). Neill and Magnuson (1974) also observed that yellow perch were less abundant in thermal plumes in all seasons than in unheated areas. Possibly a preference for low light intensity or ice cover in winter reinforces the low temperature requirements for gonad maturation and guides the fish away from the influence of onshore thermal plumes.

Temperature gradients on the spawning grounds may be a directive factor in spawning migrations of percids. Optimal temperatures for spawning and gamete viability are considerably higher than those required for maturation. Once maturation is completed, spawning migrations may be directed towards optimal spawning temperatures. In higher latitudes walleye spawning runs began while ice remained on the main lake systems. The influx of warmer water from tributary systems was a stimulus to upstream spawning migrations (Rawson 1957; Priegel 1970). In years when the water in the Gulf of Riga, Latvia, warmed up slowly, the Eurasian perch abandoned its ordinary spawning site over algae-covered stony shallows and spawned over shallow sandy banks where water temperatures were 5–8°C higher (Berzins 1949). Walleye spawning runs from Oneida Lake, New York, into Scriba Creek were blocked when creek temperatures were lower than lake temperatures (Forney 1967). Similar examples have been observed whereby spawning grounds of pikeperch have shifted with temperature changes (Bastl 1969; Biliy 1963). Significance of thermal gradients in the vicinity of spawning grounds needs to be more critically evaluated in relation to optimal temperatures for gamete viability.

Adaptations to the Seasonal Temperature Cycle

The temperature history of fish populations must be accurately described before the role of temperature in the autecology of a given species can be adequately described. A historical compendium of freshwater fisheries and water-temperature data in the continental United States was recently compiled to supplement knowledge of temperature regimes where various species were found (Hokanson and Biesinger 1977). Stations with matched fish–temperature data sets were selected only from streams, since temperature data from well-mixed water bodies would be more representative of fish-population temperature experience than data from thermally stratified waters. The most complete field and laboratory data base existed for *Perca* spp. Therefore, correlations of physiological responses and endpoints to distribution limits for this genus serves as an example for percids that have similar physiological requirements. Once ecological relationships are established, one hopes that the collection of meaningful data for other species, and useful interpretations of the existing data, will be stimulated. The seasonal temperature envelope that describes the temperature limits for adaptation of yellow perch within the United States is shown in Fig. 9. The existing field data were compiled from 35 stations in the southern part of the native range of this species. Yellow perch are found as far north as Great Slave Lake at 63° N lat., across Alberta, James Bay, Quebec, New Brunswick, and Nova Scotia (Scott and Crossman 1973). The stations sampled were primarily from the upper Mississippi River drainage and Atlantic coastal streams from Maine to North Carolina.

Temperature requirements of *Perca* spp. are superimposed on the temperature regimes where both perches were present for comparison (Fig. 9). The evaluation of temperature limits to distribution of a species cannot be based only on presence data from the species' geographical range, but must be based on formal evaluative techniques that include knowledge of life-cycle requirements and experimental introductions beyond their indigenous range (Weatherley 1977). Therefore, it is necessary to seek information on extreme temperature limits where self-sustaining populations are known to survive when introduced beyond their natural range. The warmwater regimen is from the Darling River at Bourke, which represents the lowest latitudinal limits of distribution of introduced populations of *P. fluviatilus* in Australia. The coldwater regimen is from Big Trout Lake, which is the highest latitudinal limit of distribution of *P. flavescens* in Ontario.

Requirements for reproduction and bioenergetics of a species pose ultimate limits to distribution and abundance. Seasonal fluctuations in temperature are required in percid habitat to insure that requirements for growth and repro-

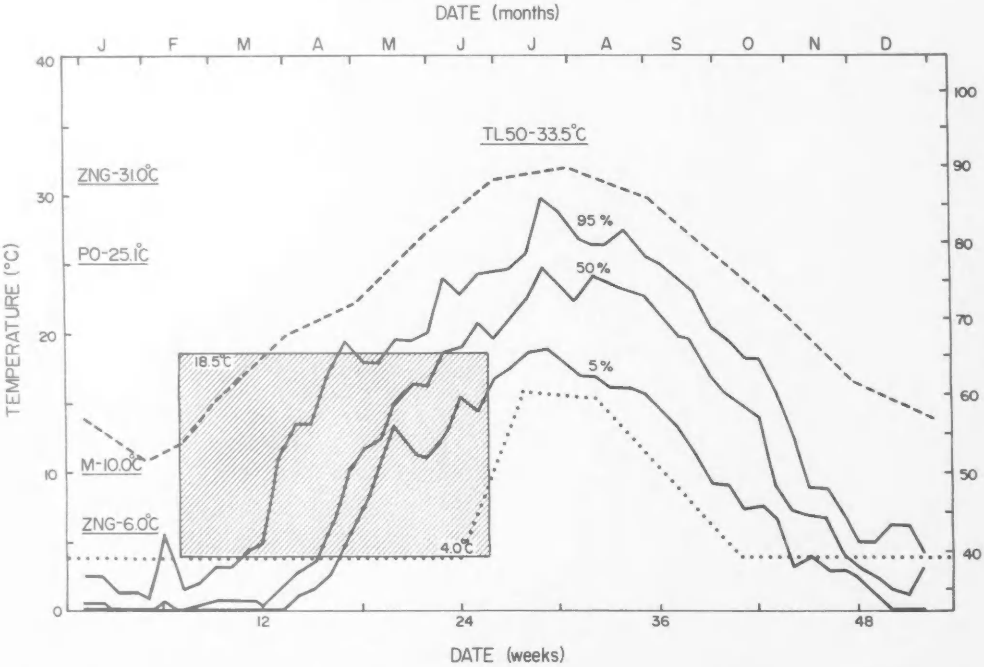

FIG. 9. Seasonal temperature envelope described by percentage occurrences ($\leqslant$) of weekly mean temperatures where yellow perch were present in 35 stream stations throughout the United States. Temperature requirements of yellow perch for physiological optimum (PO), lower and upper zero net biomass gains (ZNG), ultimate upper incipient lethal temperature (TL50), maturation (M), and spawning (shaded area) are noted for comparison (from Hokanson and Biesinger 1977). Multiple endpoints for field and laboratory observations were averaged before plotting. ------, water temperature in the Darling River at Bourke, Australia, just beyond the lower latitudinal limits of distribution of *P. fluviatilus* (from Weatherley 1963a); ......, mean monthly epilimnetic temperatures of Big Trout Lake, Ontario, from 1959 to 1964, at the higher latitudinal limits of distribution of *P. flavescens* (R. A. Ryder, Min. Nat. Resour., Thunder Bay, Ont., personal communication).

duction are met. The increasing temperature requirements of successive early life phases show how percids adapt to the spring spawning period. Spawning and gamete viability is possible from about 4.0 to 18.5°C (Fig. 9). Shifts in spawning time among perch populations are related, in part, to availability of suitable spawning temperatures for different regimes in each locality. Perch inhabiting thermal regimens corresponding to the upper envelope (95 percentile) would be expected to spawn from mid-March to mid-May. Perch inhabiting regimens corresponding to the lower envelope (5 percentile) would be expected to spawn from early May to the end of June.

There are several types of adaptation in seasonal oogenesis among percids (Koshelev 1963). In adult percids with synchronous oocyte growth and isochronous spawning (e.g. *Perca* and *Stizostedion* spp.), environmental conditions have only limited effects on the duration of the stages of gonad maturity. As a consequence, there is only a shift in the spawning temperatures and change in spawning time by only a few weeks within stocks, sometimes at the expense of gamete viability. The spawning season of perch living in a cooling pond in Poland was advanced only slightly — spawning merely proceeded at higher temperatures (12–18°C) than elsewhere (EIFAC 1968). In Lac la Ronge, Saskatchewan, walleye spawning runs began at higher temperatures (7.2–11.1°C) in years when spawning occurred early (April 30–May 7) and at lower temperatures (3.3–7.2°C) in years when spawning was delayed by cold weather (May 17–21) (Rawson 1957). In the Lake Winnebago system, Wisconsin, the walleye spawning run started sooner in the warmer tributary river marshes (2.2–15.6°C) than in the larger, colder main lake (4–11.1°C) (Priegel 1970). Greater differences in spawning time observed among stocks living at temperature extremes may be due to longer term adaptations that influence time of first maturity which also determine the start of the annual endogenous reproductive rhythm and subsequent spawning periods in each respective habitat (Hokanson and Biesinger 1977).

Pikeperch are more adaptable to changing environmental conditions than are the two perches and walleye, since their oocyte growth periods (stages III–IV) are more asynchronous (Koshelev 1963). Pikeperch in Lake Glubokoe near Moscow, USSR, accumulated nutrients in the oocytes during fall and winter. In the south these periods of oocyte growth shifted to the spring. In some reservoirs female pikeperch omitted the period of resorption and limited ova growth (stage II of maturity), an omission that is more typical of species with batch spawning. Golovanenko et al. (1970) noted asynchronous maturation of the gonads of pikeperch in different size groups. Fish of medium size matured first during the spring spawning migration. A period of supplementary feeding was needed by smaller and larger females because of the higher energy requirements associated with metabolism and high fecundity, respectively. A protracted late spring produced more synchrony in the maturation of fish used in fish culture. Bastl (1969) suggested that the pikeperch adaptation to low spawning temperature in Orava Reservoir, Czechoslovakia, could be attributed to the rich forage supply.

The reproductive cycle of ruffe is most adaptable to changing environmental conditions. The rapid and asynchronous oocyte growth and lack of a resting stage II of maturity in ruffe lead to batch spawning and longer spawning periods than in *Perca* and *Stizostedion* spp. An extended spawning period has survival value for a species by assuring that all ova do not have the same temperature history and increasing the probability that some are deposited under favorable conditions for survival.

The maturation limit (10°C) for *Perca* spp. is approached by the winter minimum temperature in Australia (Fig. 9). This temperature regime appears to be above the limits for normal maturation. The Australian population spawned only in late August, which corresponds to late February in the northern hemisphere, at temperatures above 11.5°C (Weatherley 1963a). Lake (1967a) suggested that the possible damage of oocytes by high minimum temperatures preceding spawning may be another mechanism limiting perch distribution in Australia. The effects of the longer growing season, migrations, feeding regime, and seasonal and diel temperature fluctuations on gamete maturation of stocks living at lower latitudes need to be critically evaluated. Temperatures were within acceptable levels for maturation at all U.S. stream stations and were below 10°C for 21 wk at the upper envelope (95%).

The length of the growing season may limit the northward distribution of a species through retardations of maturation of adults and growth of young. Ryder et al. (1964) showed that the natural range of yellow perch extended northward in North America to a boundary corresponding to the 16°C isotherm for mean July air temperature. The mean water temperature in Big Trout Lake, Ontario, approached this minimum isotherm (Fig. 9). The time that temperatures exceed the lower zero net biomass gain value (6°C) determines the potential length of the growing season, depending upon food availability. The Ontario population would be expected to spawn in late June and early July immediately after ice break-up. The maximum length of the growing season of yellow perch was only 15 wk. The growing season of young-of-the-year would be even shorter. The threshold for larval survival (10°C) is exceeded for only 10 wk and low winter temperatures may limit survival of smaller individuals directly, or indirectly (through predation over an extended period of no growth). Low summer temperatures may also limit reproduction through inhibition of normal resorption processes in the ovary and proliferation of the new generation of oocytes. The lower envelope (5%) exceeded the lower zero net biomass gain value for 26 wk, and maximum growth potential during the peak of the growing season was only 38% of optimum. A maximum growth potential of at least 50% in midsummer was required for a wide variety of freshwater fishes (Hokanson and Biesinger 1977). This value is represented as the generalized lower limit to fish distribution in summer in Fig. 7.

The upper zero net biomass gain temperature (31°C) may be considered an upper limit to distribution of *Perca* spp. (Fig. 7 and 9). Weatherley (1963a) showed that the natural range of yellow perch extended southward in North America to a boundary corresponding to the 31°C isotherm for mean maximum midsummer air temperature and that introduced populations of Eurasian perch in Australia were limited by the same isotherm. The Australian population had a potentially continuous growing season, except in midsummer when the temperature exceeded the upper limit of zero net biomass gain for perch populations and reduction of biomass was possible. A potential growing season of 36 wk was likely for perch populations living at temperatures approaching the upper envelope (95%). The maximum value in the upper envelope was 2–3°C above the physiological optimum for this species and it was about 3°C below the upper zero net biomass gain value for the same test. The median envelope approached the physiological optimum for this species only during the peak of the growing season. Maximum growth is not attainable throughout most of the year and growth potential can vary widely in different seasons throughout the geographical range where a species is present, depending upon temperatures in each habitat.

The lethal temperature of species provides a short-term survival mechanism to resist extreme fluctuations in environmental temperature. The ultimate upper incipient lethal temperature (33.5°C) was about 6°C above the upper envelope (95%) where yellow perch were present in the United States and 2°C above the Australian regimen (Fig. 9). Only the maximum temperature values listed in the data base by Hokanson and Biesinger (1977) approached the ultimate upper incipient lethal temperature for several fish species. In this compendium, the daily maximum temperature at the warmest station where sauger were present frequently exceeded their upper lethal temperature; the daily minimum never exceeded it. Eurasian perch were seen dying in the lower Lachlan River, Australia, during a heat wave when surface waters reached 33.3°C (Lake 1967b). Temperatures limiting distribution are always less than the upper incipient lethal temperature. Fish kills from heat are rare in nature and generally occur only when escapement is blocked or when the coolest water available to fish exceeds the lethal temperature or is deficient in oxygen.

Brett (1956) questioned whether lethality ever acted directly in influencing fish distribution and suggested that some other property or attribute correlated with the upper lethal temperature must be operating as a factor limiting fish distribution. Evidence to support his statement comes from observations that lethal temperatures are several degrees Celsius above natural distribution temperatures and that species with similar ultimate upper incipient lethal temperatures have different thermal limits of distribution in their natural habitat. Hokanson and Biesinger (1977) found a high positive correlation between the ultimate upper incipient lethal temperature and the physiological optimum and upper spawning threshold for eight fish species. If the lethal temperatures of species are correlated with ecological succession along a habitat gradient, ecological succession is also correlated with the species' basic requirements for reproduction and growth.

Thermoregulatory behavior is the mechanism by which fish stocks control their acclimatization temperature and optimize their physiological performance along a finite temperature gradient of each habitat. Close correspondence between distribution limits and temperature requirements for growth and reproduction of a species emphasizes the role of activity. The summer isotherms limiting distribution of *Perca* spp. (16–31°C) correspond closely to the range of preferred temperatures (Table 4) and distribution range in horizontal gradient tanks (McCauley and Read 1973). Multiple directive stimuli account for these broad distribution limits within and between waterbodies. The temperature range selected by perch in their natural habitat is such that positive net biomass gain will occur, insuring a sustained yield of the species. Acclimatization temperatures of all self-sustaining perch populations probably fall within these isothermal limits, even though temperature characteristics of part of their habitat may fall outside this range. Finite temperatures available to fish in a given locality provide a wide range of behavioral adaptations in waters of different temperature characteristics.

Fish adapt to different temperature characteristics by changes in their diel activity cycle and seasonal migrations. Fish adjust to the summer maximum temperature through their diel activity cycles and avoidance or preference responses. Resultant temperature fluctuations are known to be beneficial to fish populations. Benefits of diel temperature fluctuations at mean temperatures below the physiological optimum include faster growth rates and expanded scope of thermal tolerance, compared to mean constant acclimation temperatures. Brett (1971) interpreted the diel vertical migration of *Oncorhynchus nerka* as a mechanism of behavioral thermoregulation that balances daily metabolic expenditures to conserve energy when food is limited. Likewise, seasonal changes in temperature are necessary to meet the changing requirements for reproduction and growth. Seasonal migrations of percids ensure that these changing requirements in their life cycle are met. Migrations may serve to guide a population to favorable spawning temperatures, but deposited ova are subjected to uncontrolled fluctuations of nature that can determine year-class strength.

Management Implications

Management of percid communities in different latitudes must be based on knowledge of how environmental and biotic factors regulate population structure, distribution, and abundance. Species are distributed over a wide range of temperature conditions, and possibilities for population adaptation are immense. The adaptive capabilities of fish populations have been described by Beverton and Holt (1959). Data from 69 species of fish indicated a direct relationship between growth rate and mortality rate and maximum age and asymptotic length, and inverse correlations between maximum age and mortality rate and asymptotic length and growth rate. Comparisons with environmental data indicate that growth rate is affected by temperature and that asymptotic length is affected by food and temperature. Comparisons of the ratio of length at maturity to asymptotic length with maximum age suggest high ratios related to short life span. Reproductive drain is evident with fast growth and early maturity. Tanasiychuk (1974) and Colby et al. (1977) also observed a relation between fast growth rates, early maturity, and short life span in pikeperch and walleye. Southern populations are typified, relative to northern stocks, by accelerated growth and higher fecundity.

The background data for percids presented herein provides the basis for formulation of a hypothesis concerning stock variability in response to environmental temperature. It is acknowledged that local biotic and abiotic variables can mask any correlations with temperature within any given waterbody. Therefore, maximum expression of the temperature factor can be observed at geographical extremities of a species range. All variables that influence percid population dynamics and structure are assumed to be constant or not limiting, so that the controlling influence of temperature can be compared. The three acclimatization temperatures illustrated in Fig. 9 are the driving variables for the following predictions:

1) Coldwater regimen (lower envelope). This population is characterized by low rate of recruitment attributed to poor survival of larvae in summer and of the young over winter. Growth is slow and confined to summer. Age of maturity is high. Natural mortality of older age-groups is low; consequently populations consist of multiple age-groups and longevity is highest. Population may be distributed in surface waters throughout summer. Population biomass may be high in virgin stocks, but population resiliency is low.

2) Median envelope. This population has a variable rate of recruitment, depending on rate of temperature increase throughout the spawning season and food available for larvae. Growth rate is intermediate and limited to the postspawning period through early fall. Age of maturity, longevity, and number of age-groups are intermediate. Population is in surface waters in spring and early summer with gradual migration to deeper waters, older age-groups migrating first. Population biomass and resiliency is highest.

3) Warmwater regimen (Australian regimen and upper envelope). Recruitment is low and limited by proportion of females that mature and spawn and by high spawning temperatures that reduce gamete viability. Survival of larvae and young is limited by food supply and predation. Growth rate is high with a prolonged growing season from spring to fall, except for the warmest period in summer. Age of maturity is low. Natural mortality rate is high among all age-groups. This population is composed of a few age-groups and longevity is least. Percid distribution in summer is restricted to cold-water refugia such as the thermocline or hypoclimnion, which are less productive zones and occupy a smaller area of the waterbody. These stocks are most vulnerable to cultural eutrophication and exploitation. Population biomass is lowest.

These predictions emphasize the long-term and continuous influence of temperature history on percid population dynamics and structure. It is recognized that local factors, such as community relationships and morphoedaphic factors, can mask these trends. These temperature regimens would be expected to exert a different influence on species with requirements unlike those of percids. Population density and competition would exert their influence through limitations on food availability. Predation can be viewed as the relative influence of temperature on the appetite and activity of the predator in respect to its influence on growth and activity of the prey. The role of temperature in shaping aquatic communities is implicated through its effect on the relative population dynamics of each respective species and on species interactions.

The hypothesis should be verified by several approaches before management strategies are formulated:

1) Describe population dynamic characteristics and limnological conditions at geographical extremities of a species' range.

2) Derive population dynamic models to describe how a fish crop develops as a function of time for different temperature regimens (Kitchell and Stewart 1977).

3) Document changes in population dynamics and community structure at different temperature regimens in experimental ponds or streams.

The implications for management based on these predictions are the following:

1) Mechanisms of population regulation are different for each temperature regimen. Temperature effects are multiple, instantaneous, and cumulative.

2) Population resilience to forces of exploitation and cultural eutrophication varies in cold- and warmwater regimens. Populations living at mid-range or median regimens would be expected to be most resilient to exploitation and environmental degradation.

3) Pollution and community interactions exert similar effects as temperature on populations, and proper interpretation of cause–effect relationships requires thorough knowledge of temperature requirements of each species.

4) Management regulations cannot be universally applied for a given species throughout its geographical range.

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Development and Food of Age-0 Eurasian Perch (*Perca fluviatilis*) in Reservoirs near Moscow, USSR[1]

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SPANOVSKAYA, V. D., AND V. A. GRYGORASH. 1977. Development and food of age-0 Eurasian perch (*Perca fluviatilis*) in reservoirs near Moscow, USSR. J. Fish. Res. Board Can. 34: 1551–1558.

Eurasian perch (*Perca fluviatilis*) spawned in Mozhaisky and Uchinsky reservoirs in early May when water temperatures were 5–10°C. Larvae subsisted on the yolk sac until the mouth became terminal at 6.0–7.0 mm standard length. Larval development is illustrated by drawings and discussed. As young perch grew they fed on cladocerans in preference to copepods, later switching to insect larvae. Daily ration of larvae in June was 12–16% body weight and of fingerlings 5–28% body weight, in different months and years. Most feeding was crepuscular. In the years when food was abundant fast-growing young-of-the-year matured as precocious males in autumn. They spawned with larger females the following spring. This is considered to be an adaptive response to increased food supply and low population densities.

Key words: Percidae, *Perca*, food, development, spawning, Mozhaisky Reservoir, Uchinsky Reservoir

SPANOVSKAYA, V. D., AND V. A. GRYGORASH. 1977. Development and food of age-0 Eurasian perch (*Perca fluviatilis*) in reservoirs near Moscow, USSR. J. Fish. Res. Board Can. 34: 1551–1558.

La perche aurasienne (*Perca fluviatilis*) fraye dans les réservoirs Mozhaisky et Uchinsky au début de mai au moment où les températures de l'eau sont de 5 à 10°C. Les larves subsistent à même la vésicule jusqu'à ce que la bouche devienne terminale à 6.0–7.0 mm LS. Nous examinons le développement larvaire que nous illustrons par des dessins. A mesure qu'elles croissent, les jeunes perches se nourrissent de cladocères de préférence aux copépodes, pour ensuite se tourner vers les larves d'insectes. La ration quotidienne des larves en juin est de 12–16% du poids corporel; celle des fingerlings de 5–28% du poids corporel, selon le mois et l'année. L'alimentation a lieu surtout au crépuscule. Durant les années où la nourriture est abondante, les jeunes de l'année à croissance rapide atteignent la maturité comme mâles précoces en automne. Ils frayent avec les femelles plus grandes au printemps suivant. Ceci est considéré comme une réponse adaptive à une augmentation des approvisionnements en nourriture et à de faibles densités de population.

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THE perch is an adaptable species as evidenced by its broad distribution. Part of this adaptability is to be found in the variations in development and in changing food habits of age-0 perch. Our purpose is to describe spawning dates, development, and food habits of age-0 perch in reservoirs near Moscow. Special emphasis is given to the occurrence of precocious males in certain years.

Materials and Methods

Our study was conducted in three reservoirs near Moscow, USSR. Mozhaisky Reservoir is 31 km^2 and drains 1360 km^2, Rouzsky Reservoir is 32 km^2 and drains 1150 km^2, and Uchinsky Reservoir is 19 km^2 and drains 42 km^2. Their average depths are 6–7 m.

We studied Mozhaisky Reservoir each year from 1960, when the Moscow River was dammed, until 1974. In the other two reservoirs observations were irregular, but samples in Rouzsky Reservoir were taken just after the basin was created in 1966–67. The small Uchinsky Reservoir at the junction of the Rivers Ucha and Vyasa was created in 1937, and our observations were made long after its formation. Water levels in Mozhaisky and Rouzsky reservoirs

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vary greatly during the year, but they are more nearly stable in Uchinsky Reservoir.

Larval perch were collected with a conical silk net (1-mm mesh, mouth diam 30 cm) in the littoral zone and with an egg net (1-mm mesh, mouth diam 60 cm and length 120 cm) in open water. Fingerlings were collected with a 12-m trawl with appropriately small mesh. We sampled zooplankton in summer with a 4.5-ℓ Patalas trap in bays and a conical net with 0.16-mm mesh in open water. Samples were preserved in 4% formalin. In bays 10 samples were taken at each station and filtered through a 0.16-mm mesh screen.

Standard length (SL) and weight of fishes were measured and sexes of those longer than 35 mm SL were determined. Sex could be distinguished by the histological examination of gonads when fish reached 8.2–12.5 mm SL. Sex was distinguished by the anatomical structure of the gonads when fingerlings were 35 mm or longer. Contents of the stomach were weighed. Weights of individual food items were estimated directly by volume, or indirectly from tables of standard weight when only fragments were present. Weight of each component or item is given as percent of the total weight of food.

Food of perch fingerlings is analyzed for several years to show food specificity. The importance of each item in the diet was estimated as the frequency of occurrence of samples with a given item and as frequencies of occurrence of the samples with few (⩽10%), intermediate (11–49%), or abundant (⩾50%) quantities of an item judged by percent of stomach content by weight.

Daily rations of perch larvae and fingerlings were determined. Larval or fingerling perch were taken from the reservoir at approximately 3-h intervals over 24-h periods in June 1972 and July 1960, 1969, and 1972. Weights of food in the stomach were averaged on a per fish basis and expressed as a percent of body weight.

As an example, we calculated the daily ration of a perch fingerling (Table 1). In this case, the fingerling consumed primarily cladocerans and copepods. We assumed that the two foods were digested at the same rate and estimated digestion rate by the decline in food content after the fingerling stopped feeding at 2100. We calculated the quantity of food passing through the digestive tract from 2100 to 0000 as 3.46% − 1.19% = 2.27% of body weight, or 0.76%/h. Using this digestion rate, the daily ration for July 24–25 was calculated to be 15% of body weight (Table 1).

Daily rations of larvae over several years were determined by methods of Winberg (1956).

TABLE 1. Sample calculation of daily ration for fingerling perch in Uchinsky Reservoir on July 24–25, 1959.

Time (h)	Content of stomach + intestine (% of body wt)	Food consumed[a] (% body wt)
1300	3.58	3.58
1500	3.15	1.09
1800	4.30	3.42
2100	3.46	1.43
0000	1.19	0
0300	1.33	1.33
0600	1.90	2.84
0900	1.07	1.44
1200	1.03	0
Total		15.13

[a] Stomach content plus food digested since last observation minus stomach content at last observation. For example, between 1500 and 1800, ration = 4.30% wt + (3 h × 0.76% wt/h) − 3.15% wt = 1.09 body wt.

TABLE 2. Dates of spawning by perch in Mozhaisky and Uchinsky reservoirs in relation to water temperatures and water levels in various years from 1958 to 1974.

Year	Avg water temp (°C) 1st 10 days of May	Water level	Date of spawning		Length of spawning season (days)
			First	Last	
		Mozhaisky Reservoir			
1963	10.4	High	May 8	May 20	12
1966	11.2	Middle	3	20	17
1967	6.8	Middle	9	25	16
1968	7.5	High	10	June 10	31
1969	4.9	Low	9	14	35
1970	9.5	Very High	13	19	36
1972	5.6	High	5	5	31
1973	9.7	Low	8	May 21	13
1974	6.3	Very High	12	23	11
		Uchinsky Reservoir			
1958	8.0	Stable	10	20	10
1971	8.0	Stable	8	June 5	28

TABLE 3. Age compositions of spawning perch (percent) in Mozhaisky and Uchinsky reservoirs in various years from 1958 to 1971.

Year	Age										No. of fish
	2	3	4	5	6	7	8	9	10	11	
					Mozhaisky Reservoir						
1963	10	60	10	—	—	16	4				84
1966	5	45	20	4	20	3	3				100
1968		20	12	32	16	9	7	4			199
1969		6	26	31	24	8	4	1			285
					Uchinsky Reservoir						
1958	8	35	49	5	2	1					108
1971	22	6	41	13	6	6	0	2	2	2	70

Spawning and Development

Spawning dates — Perch in Mozhaisky and Uchinsky reservoirs usually began to spawn during the first 10 days of May, when water temperature averaged 5–10°C. The spawning dates depended on hydrological conditions (Table 2) and age composition of the spawning stock (Table 3). In the 1963 spawning population, age-3 fish, or the year-class formed during the 1st yr of flooding, predominated. Water levels were high and the spawning period was exceedingly short. From 1968 to 1972 the spawning season lengthened as perch increased in abun-

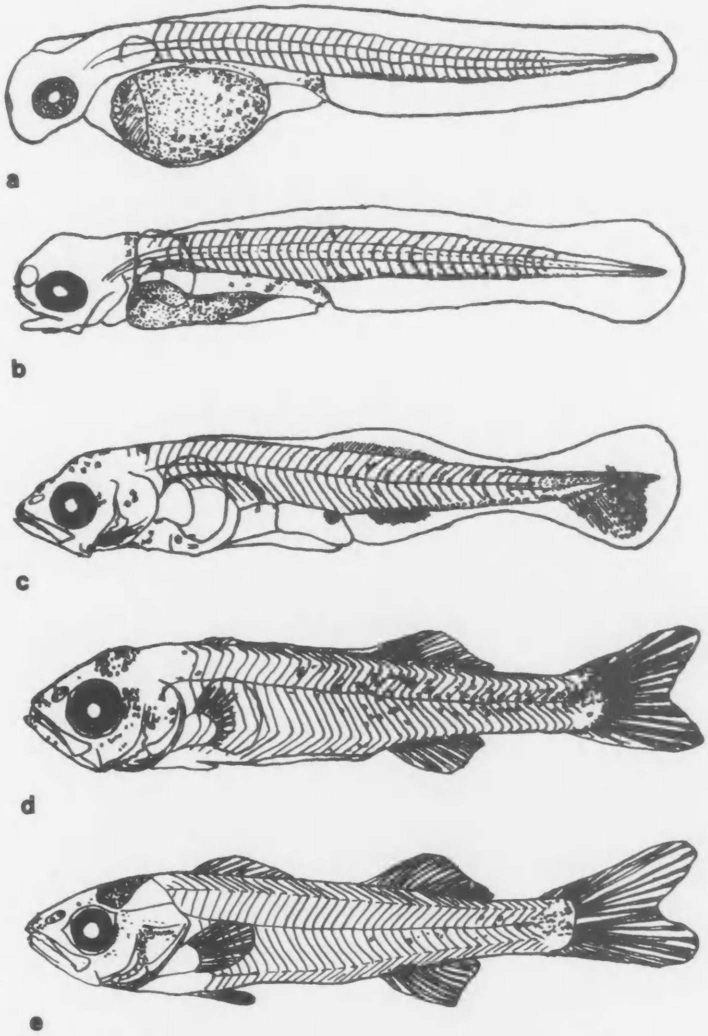

FIG. 1. Development of perch during larval period (Konstantinov 1957): a, stage I; b, stage III; c, stage V; d, stage VII; and e, stage VIII.

dance and more age-groups were spawning (Spanovskaya et al. 1973). At the high temperatures recorded in 1966–67 the spawning period was shorter than in the next year. As the total abundance of perch sharply declined in 1973–74 the spawning period again shortened. However, spawning began at the same time in the two reservoirs.

Larval development — Early developmental stages of perch were distinguished as larvae (stages I–VIII) and fingerlings (stages IX–X) (Kryjanovsky et al. 1953; Konstantinov 1957; Dmitrieva 1967).

After hatching the larva subsists on its yolk sac and has no mouth or branchial apertures, and the body is fringed with a continuous median fin fold (stage I, Fig. 1a, 2a, and 3a). At stage II the mouth appears in an inferior position, branchial arches are laid down, pectoral fins increase in size but have no rays, and caudal lobe of median fin fold is separated. At lengths of 6.0–7.0 mm (stage III) the mouth becomes terminal and the larva begins active feeding (Fig. 1b).

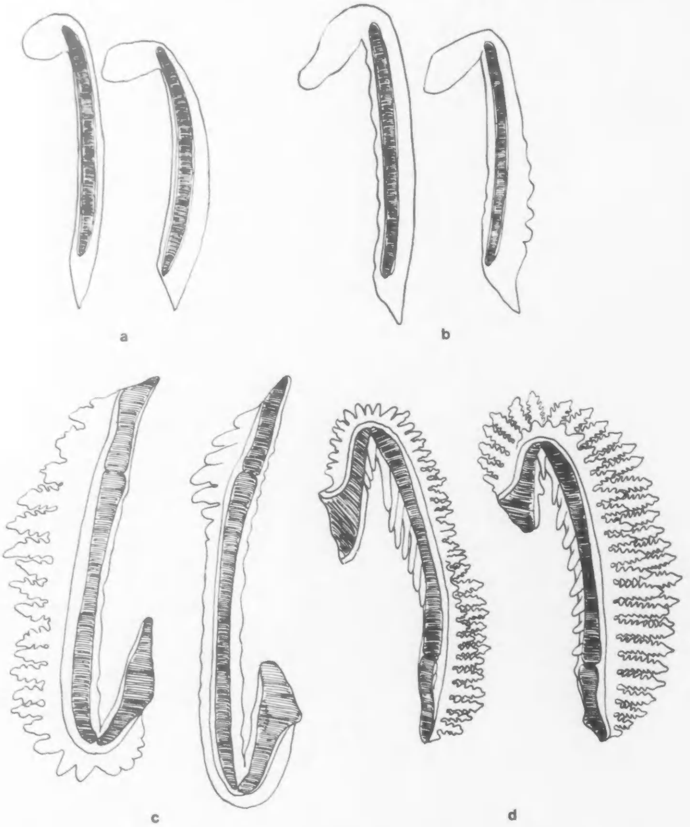

FIG. 2. Development of the first and second gill arches of perch during larval period (Konstantinov 1957): a, stage I; b, stage III; c, stage V; d, stage VII.

The fish now gains nourishment from both active feeding and the yolk sac. Bases of gill filaments appear on the second branchial arch, and minute projections (future gill rakers) become visible on the inner surfaces of branchial arches (Fig. 2b). The anterior, middle and posterior portions of intestinal tube are formed, and the swimbladder appears, connected to the esophagus through the ductus pneumaticus (Fig. 3b).

At succeeding stages (IV–VIII) the larva grows to a length of 15–18 mm (Fig. 1c–e). The median fin fold gradually is replaced by median fins, lepidotrichii develop in all fins (median and paired), the swimbladder is filled with air and loses its connection to the esophagus, separate elements of branchial arches are formed, gill filaments develop on other branchial arches, teeth appear on the jaws, and pyloric appendages become visible. The larva at these stages becomes mobile and its orientation ability improves with the development of sense organs (Fig. 2c, d; 3c, e). Thus the larva becomes a fingerling which looks like a diminutive adult (stages IX and X).

At stage IX (length 18–28 mm) the stomach increases to form a large sac, the third and fourth intestinal loops appear, pyloric appendages enlarge significantly, scales appear on the postanal portion of the body and soon afterwards cover the whole body. Simultaneously (especially at stage X), the number of conductive tissues in the brain greatly increases, cavities in the optic lobes and saccus vasculosus enlarge, the seismosensory body canal is closed and their orientation ability is greatly improved. The fingerling period usually ends at a length of 50–80 mm.

Larval perch (stages I–VIII) occur in Mozhaisky Reservoir from May to the beginning of July.

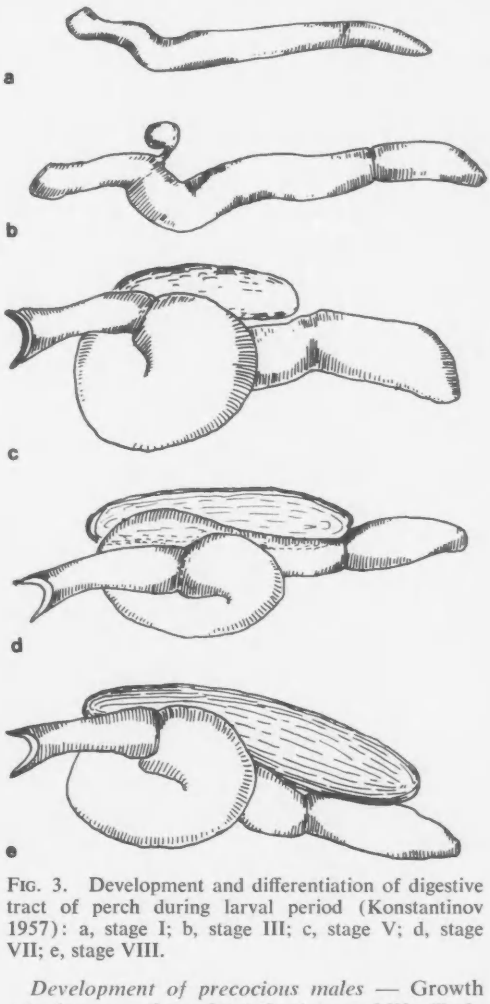

FIG. 3. Development and differentiation of digestive tract of perch during larval period (Konstantinov 1957): a, stage I; b, stage III; c, stage V; d, stage VII; e, stage VIII.

Development of precocious males — Growth rate decreases throughout the 1st yr of life. Early larvae grow from 0.08 to 0.11 mm/day, but later only 0.03 to 0.05 mm/day. Older fingerlings slow to 0.003–0.007 mm/day. Growth in weight declines in a similar way. Considerable variation occurs in the length and weight of fingerlings. Variation is associated with environmental and feeding conditions, such as differences in time of spawning, temperature variation, and food abundance. As a result, in the autumn young perch vary in length, weight, condition factor, and the development of gonads (Table 4). The highest values were observed in 1960, high ones in 1972 and 1973, average ones in 1966, and rather low values in 1968 and 1969.

In years when fingerling growth was rapid, the testes of some reached stage IV of maturation by autumn of their 1st yr of life. Despite the small size of these precocious males relative to older spawners, they participate in spawning when 1 yr old. Precocious males occurred at 1 yr of age in years of good growth (Table 4).

TABLE 4. Average lengths, weights, and condition factors of perch fingerlings during September in Mozhaisky Reservoir and occurrence of precocious males in various years from 1960 to 1974.

Year	Length (mm)	Weight (g)	Condition factor[a]	Years with precocious males	*n*
1960	77.0	8.44	1.88	+	70
1966	58.0	2.90	1.49		20
1967	69.0	5.12	1.58	+	5
1968	52.0	2.05	1.45		116
1969	54.0	2.20	1.40		106
1972	64.5	4.80	1.80	+	240
1973	64.0	4.40	1.65		5
1974	57.0	3.50	1.62	+	36

[a](Weight ÷ length) (100).

Average lengths and weights of juvenile males and females were highly variable. Precocious males were larger and they varied less in length than their cohorts (Table 5). In the autumn samples, sex ratio was approximately 1:1. Males predominated in spring samples on the spawning grounds when precocious males were numerous. The condition factor of the precocious males is also somewhat higher (Table 5). Thus, perch differ in growth and rate of maturation as early as the 1st yr of life.

Food and Daily Ration

Food of larvae and fingerlings — The main food of larval perch was cladocerans (Table 6). *Daphnia* and *Chydorus* spp. predominated and were abundant in the littoral zone. Copepods were also common in stomachs but were less

TABLE 5. Lengths, weights, and condition factors (mean and SD) of juvenile males, juvenile females, and precocious males in Mozhaisky Reservoir in 1972. Numbers in parentheses are sample size.

Characteristic	Juvenile females (63)	Juvenile males (36)	Precocious males (28)
Length (mm)	65.8±0.6	63.7±0.78	70.7±0.8
Weight (g)	5.02±0.18	4.31±0.15	6.34±0.26
Condition factor	1.72±0.01	1.70±0.01	1.77±0.02

TABLE 6. Percentage compositions (by weight) of food items of larval perch at stages VI–VIII in Mozhaisky Reservoir.

	Developmental stage (length in mm)			
Item	VI	VII (13–15)		VIII (16–18)
Sample size (no. of fish)	13ᵃ	10ᵇ	11ᶜ	75ᵈ
Stomach fullness (% of body wt)		0.89	1.19	2.25
Cladocera				
Daphnia	50	32	15	62
Bosmina				1
Chydorus	34	10	82	1
Leptodora		13		
Scapholeberis	1			
Copepoda				
Cyclops, Mesocyclops	8		3	5
Copepoditi		45		
Harpacticoida				<1
Chironomid larvae	7			6
Chironomid pupae				25

[a]1970; [b]1966; [c]1967; [d]1972, from a diel sample series.

prominent than cladocerans. Chironomid larvae and pupae were less common than copepods. They were represented mostly by littoral forms of the second and third instars of genera such as *Cricotopus* sp., *Tanytarsus* sp., and *Psectrocladius* sp.

The main food of fingerlings (stage IX) was also cladocerans (Tables 7 and 8). The most common were *Daphnia* spp., *Bosmina* spp., and *Leptodora kindti*, all of which were abundant in open water and in the littoral zone. Littoral forms such as *Sida crystallina*, *Limnosida frontosa*, and *Chydorus spaericus* were less important copepods, and larvae and pupae chironomids were more important to fingerling than to larval perch. Hemiptera and fishes also occurred in the stomachs. Young perch preyed infrequently on smaller larvae of perch and some cyprinids.

Predation on larval and fingerling perch was also observed by us in some bays of Mozhaisky Reservoir, in lakes during high water in the spring (Spanovskaya and Grygorash 1962), and in artificial ponds (Il'ina 1973) where the density of young fish was high. Vulnerability to cannibalism occurred at lengths of 13 mm (this study) and 10–11 mm (Il'ina 1973).

The prevalence of items in the diet was related to their abundance and ability of perch fingerlings to select them. Comparison of the species composition of zooplankton and the stomach contents of fingerlings from Khotilovsky Bay of Mozhaisky Reservoir revealed that fingerlings selected larger prey. The most abundant zooplankton in bays were copepods (95.5% of weight), mainly nauplii and copepodites. Determinations after Ivlev (1961) indicate that fingerlings almost entirely ignored them ($E = -0.15$) but selected adult *Mesocyclops leucarti* ($E = +0.8$) and *Daphnia longispina* and *D. culcullata* ($E = +0.9$).

Grese (1939) found that fingerlings selected only certain plankters. Larger fingerlings ate larger prey (Table 8), selecting large forms such as copepods or cladocerans. The importance of cladocerans in the diet of fingerlings relates to the seasonal dynamics of the plankters. Cladocerans are most abundant later than copepods — usually during June and the first half of July. Zooplankton remains important as the fingerlings grow, but the importance of cladocerans declines, and insect larvae, especially chironomids, increase (Table 7).

The predominance of zooplankton, nekton, or benthos in the diet of perch fingerlings is determined by the relative abundance of these items. Cladocera were important to perch fingerlings during rich zooplankton blooms in 1960 and 1972 in Mozhaisky Reservoir, as indicated below:

Year	Zooplankton biomass (g/m³)	Daily ration (% body wt)
1960	2.3	28
1972	1.7	15
1969	0.2	7

Insect larvae and small fish increased in the diet of perch fingerlings when zooplankton was scarce, especially in 1967 and 1969.

Perch fingerlings frequently occurred with fingerlings of other young percids, such as ruff (*Gymnocephalus cernua*) and pikeperch (*Stizostedion lucioperca*). Perch and ruff fingerlings fed mostly on chironomid larvae (Table 9). The food similarity values (Shorygin 1952) for ruff and perch fingerlings were 63 and 25%. The similarity index was the least of the two percentages for the same food items in each species. Young ruff utilized the forms inhabiting the substrate, *Chironomus* spp., *Crytochironomus* gr. *defectus*, and *Polypedilum* spp., more intensively than did perch fingerlings. Young ruff consume more chironomid larvae than do perch. Pikeperch and perch differ considerably in their food habits, since perch consume fewer young fishes of other species. Pikeperch consume mainly small perch fingerlings.

Daily rhythm and food ration — Feeding by perch larvae and fingerlings varies in intensity during a 24-h period (Fig. 4). Perch nearly stop feeding at night. During the first half of the summer, when day length is 18–19 h, feeding is maximum early in the morning and in the evening. Occasionally perch feed only in the evening (1900–2200). Such daily feeding rhythms are common when perch consume zooplankton (Fig. 4). As day length decreases in autumn, the benthos constitutes an important portion of the diet of young perch and maximum feeding occurs during morning.

TABLE 7. Frequencies of occurrence (percent) of food items of stage IX (17–28 mm) and stage X (31–62 mm) fingerling perch in Mozhaisky Reservoir during 1966, 1967, 1970, and 1972. Stage IX percentages are based on 15 samples of 600 specimens each, those of stage X on 16 samples of 630 specimens each. (Note percent of total samples, not the percent of individual fish.)

	Abundance in stomach (% by wt)[a]							
	Stage IX				Stage X			
Food items	Few	Intermediate	Abundant	All 15 samples	Few	Intermediate	Abundant	All 16 samples
Cladocerans	13	20	67	100	19	56	25	100
Copepods	50	43	7	93	32	56	12	100
Chironomid larvae	40	40	20	67	30	40	30	81
Chironomid pupae	67	33	—	60	82	18	—	69
Hemipterans	100	—	—	20	75	25	—	25
Other invertebrates	—	—	—	—	60	40	—	31
Fish	—	50	50	13	—	50	50	13

[a] Few ≤ 10% weight of contents; intermediate = 11–49%; abundant ≥ 50%.

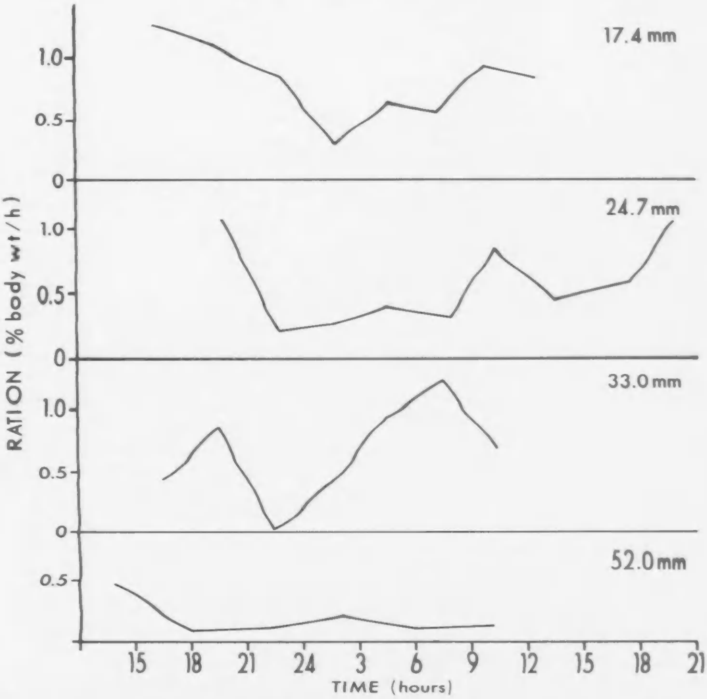

FIG. 4. Daily feeding rhythms of perch larvae (17.4 mm on June 11–12, 1972) and perch fingerlings (24.7, 33.0, and 52.0 mm on July 3–4 in 1969, 1972, and 1960, respectively). The principal food components were *Daphnia* sp(p). for larvae and cladocerans and chironomid larvae for fingerlings.

Daily rations of fingerlings varied from 7 to 28% of body weight from year to year depending on the food supply. The daily ration of larvae reaches 12–16% body weight in June. Daily ration of perch fingerlings fluctuates from 7 to 13% in July and from 5 to 8% in August and September. Perch can consume larger amounts of food. In 1960, when zooplankton was unusually abundant, the ration in early July reached 28%; however, this is uncommon.

TABLE 8. Percents of fingerling perch of several lengths containing zooplankton of various lengths in their diets in Mozhaisky Reservoir in June 1966.

Length of fingerlings (mm)	*n*	*Chydorus* (0.5 mm)	*Cyclopoida* (0.5–0.6 mm)	*Diaptomus* (1.5 mm)	*Daphnia* (1.8–2.0 mm)	*Leptodora* (2.0 mm)
16–21	12	15	45	—	32	8
26–27	30	10	22	—	65	13
29–32	15	—	—	36	45	19

TABLE 9. Food compositions (percent by weight) of fingerling perch, pikeperch, and ruff in bays of Mozhaisky Reservoir in July 1967 and 1974.

	July 1967		July 1974	
Species	Perch	Ruff	Perch	Pikeperch
Length (mm)	34–45	30–43	26–46	34–52
No. of fish	31	27	56	22
Chironomid larvae	58	95	73	12
Chironomid pupae	4	0	< 1	< 1
Cladocerans	19	4	23	13
Copepods	11	1	4	< 1
Other invertebrates	8	0	0	0
Fish	0	0	0	74.4

Discussion

The food pattern of larval perch in the study reservoirs is typical for waters of the eastern USSR (Zhitlo 1939; Krivobok 1952; Luferov 1960; Fenjuk 1960; Postnov and Prozorova 1963). The euryphagous ability is a characteristic feature of the young perch. Even the progeny in an experimental pond from the same pair of spawners exhibited differences in stomach contents and feeding pattern (shoaling plankton-eaters, benthos-eaters, and individual predators) and occupied different ecological niches (Il'ina 1973).

In our view, occurrence of precocious males is favored by an abundant food supply for larvae at the stage of mixed feeding because this favors greater survival of larvae differing in physiological characteristics. Abundant food at successive stages in the development of young fish provides high growth rates and high condition. This often occurs when recruitment is low. Also, after a river is dammed, a small river population finds favorable conditions in large flooded areas which provide abundant food. These precocious males spawn with larger females. Precociousness may be considered as an adaptive response of the species to a decrease in population size and an increase in food supply.

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Food and Feeding Relations of Eurasian Perch (*Perca fluviatilis*) and Pikeperch (*Stizostedion lucioperca*) in Various Waters of the USSR[1]

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Popova, O. A., and L. A. Sytina. 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish. Res. Board Can. 34: 1559–1570.

Eurasian perch, *Perca fluviatilis*, and pikeperch, *Stizostedion lucioperca*, are the most widely distributed of the 11 species of percids in the USSR. This literature review examines their feeding ecology in the USSR.

The pikeperch is an ambush–pursuit predator. It can become piscivorous within a few months after hatching, when it begins feeding mostly on small pelagic schooling fishes. In contrast, the perch, a facultative ambush predator, hunts during the day, eating mostly invertebrates and young fish.

The daily ration of pikeperch during the most intensive feeding period constitutes 4.5–5.5% of the body weight and decreases to 0.5% during periods of less intensive feeding. The annual ration is 200–250% of its body weight. About 60% of the annual ration is consumed during spring, 15% during summer, 22% during autumn, and 3% during winter. The daily ration of perch is similar to pikeperch — 1–4% of the body weight during spring and autumn and 0.5% during other months. The annual ration of perch is 175–200% of its body weight. About 40% of the annual ration is eaten during spring, 30% during summer, 15% during autumn, and up to 20% during the winter. The conversion of wet weight of food eaten to wet weight of predator is higher for pikeperch (19.6%) and perch (18.2%) than for other predators in our area.

Due to different feeding conditions the biological roles of perch and pikeperch vary even within the same water body. Adult pikeperch are always piscivorous, but perch often compete with other fishes for food and are a source of food for pikeperch and other large predators. The abundances of perch and pikeperch are inversely related; a decrease in pikeperch leads to a sharp increase in perch. In some small lakes in the forested area of northwest USSR, the fish fauna is represented by only two sizes of perch: small ones feeding on zooplankton and benthos near shore and larger ones cannibalizing the small ones; these two forms have fluctuated with 17-yr cycles.

Calculation of diel, monthly, and annual rations of predators made it possible to determine the total food consumed in a year by one fish and by an entire stock of these predators. Stocking with pikeperch to control smaller fish abundance has been successful in waters with rich food supplies, but in some lakes of Middle Asia it annihilated the native fish fauna.

Key words: Percidae, feeding habits, *Perca*, *Stizostedion*, annual rations

Popova, O. A., and L. A. Sytina. 1977. Food and feeding relations of Eurasian perch *Perca fluviatilis*, and pikeperch *Stizostedion lucioperca* in various waters of the U.S.S.R. J. Fish. Res. Board Can. 34: 1559–1570.

Des onze espèces de percidés de l'U.R.S.S., la perche eurasienne, *Perca fluviatilis*, et le sandre, *Stizostedion lucioperca*, sont les plus largement répartis. La présente revue de la littérature examine leur écologie alimentaire dans l'U.R.S.S.

Le sandre est un prédateur d'affût et de poursuite. Il peut devenir piscivore en moins de quelques mois après l'éclosion, alors qu'il commence à se nourrir surtout de petits poissons formant des bancs pélagiques. Par contraste, la perche, un prédateur d'affût facultatif, chasse durant le jour, se nourrissant surtout d'invertébrés et de jeunes poissons.

La ration quotidienne du sandre durant la période d'alimentation la plus intensive constitue 4.5–5.5% du poids corporel et diminue à 0.5% durant les périodes d'alimentation moins intensive.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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La ration annuelle est de 200–250% de son poids corporel. Il consomme environ 60% de sa ration annuelle au printemps, 15% en été, 22% en automne et 3% en hiver. La ration quotidienne de la perche est semblable à celle du sandre — 1–4% du poids corporel au printemps et en automne, et 0.5% durant les autres mois. La ration annuelle de la perche est de 175–200% de son poids corporel. Elle absorbe environ 40% de sa ration annuelle au printemps, 30% en été, 15% en automne et jusqu'à 20% en hiver. La conversion du poids humide de nourriture absorbée en poids humide du prédateur est plus élevée chez le sandre (19.6%) et la perche (18.2%) que chez les autres prédateurs de notre région.

Par suite de conditions différentes d'alimentation, les rôles biologiques de la perche et du sandre diffèrent, même dans un même plan d'eau. Le sandre adulte est toujours piscivore, mais la perche est souvent en compétition avec les autres poissons pour la nourriture et est une source de nourriture pour le sandre et autres grands prédateurs. L'abondance de la perche est en relation inverse de celle du sandre; une diminution du sandre entraîne une abrupte augmentation des perches. Dans certains petits lacs de la région boisée du nord-ouest de l'U.R.S.S., la faune ichtyologique n'est représentée que par deux tailles de perches : des petites qui se nourrissent de zooplancton et de benthos près du rivage et de plus grandes qui exercent un cannibalisme sur les plus petites perches; ces deux formes ont subi des fluctuations en cycles de 17 ans.

En calculant les rations quotidiennes, mensuelles et annuelles des prédateurs, il a été possible de déterminer la quantité totale de nourriture consommée en une année par un poisson et par un stock entier de ces prédateurs. L'ensemencement de sandres dans le but de contrôler l'abondance de poissons plus petits a réussi dans des eaux riches en nourriture, mais dans certains lacs de la Moyenne-Asie, de tels ensemencement annihilèrent la faune ichtyologique indigène.

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IN the USSR the percids are represented by 10 species of five genera: *Stizostedion* (*Lucioperca*), *Perca, Zingel, Percarina,* and *Gymnocephalus.* The species of some genera are rare: *Zingel* (two species), *Percarina* (one), and *Gymnocephalus* (two). They occur only in the European region of the USSR, in lower reaches of rivers flowing into the Black and Azov seas. Two species of *Stizostedion* inhabit areas of the Black and Caspian seas; the freshwater form, *S. volgensis*, is scarce, but the marine form, *S. marina*, is common. *Perca schrenkii* occurs only near lakes Balkhash and Alakol (Svetovidov and Dorofeeva 1963).

Only three percids are widely distributed and abundant in the temperate zone of Eurasia. These are the pikeperch, perch, and ruffe (*G. cernua*). The first two species have close relatives in North America. All three belong to a different faunistic complex (Nikolsky 1953a; Yakovlev 1964) and are related by their feeding ecology despite considerably different life histories. Pikeperch inhabits rivers and lakes of the USSR in regions of the Baltic, Black, Azov, Caspian, and Aral seas. It occurs from 64°N in Swedish and Finnish waters to the Caucasus Ridge and Aral lakes in the south and from the Elbe and Maritsa in the west to waters of mid-Asia in the east. Near Lake Baikal its fossils have been found in Miocene deposits (Yakovlev 1964). Its present range has expanded considerably into mid-Asia and Siberia. Perch is even more widely distributed and dwells in diverse waters throughout Europe. It occurs from the northern rivers running into the sea to mid-Asia and reaches the Kolyma River in Asia. At present it does not occur in the Amur River basin, but it did during the Miocene, as evidenced by paleontological data (Yakovlev 1964). Ruffe is as widely distributed as perch.

Among the percids, the perch and the pikeperch are ecologically significant predators in temperate waters of Eurasia and are of importance to the fishery. They have a high biomass and represent the third or fourth trophic level. Ruffe is usually regarded as forage for perch and pikeperch.

The purposes of our paper are to describe the general feeding ecology of perch and pikeperch, to compare their food habits, daily rations, and seasonality of feeding among water bodies of different latitudes, and to consider the importance of these predators on community structure of waters in the USSR. Materials are from a review of the literature and, in some cases for the Volga Delta, from a new analysis or summary of data used in preparing Fortunatova and Popova (1973). Other primary references used for comparisons are the studies by Ivanova (1965, 1968a, b) on Rybinsk Reservoir, by Pihu and Pihu (1974) on Pskov-Chudskoy Lake, and by Kudersky (1961a, 1962) on the Karelian Lakes.

Feeding Habits

The pikeperch, up to 130 cm long and 15 kg in weight, is rheophilic and has specialized habitat requirements. It lives only in large bodies of water that are well oxygenated and where food is abundant, such as deep streams and open areas of lakes and reservoirs. This accounts in part for its having a narrower range than perch or ruffe (Kudersky 1961b). Both freshwater and semi-anadromous forms are found.

The pikeperch is an ambush–pursuit predator that feeds at low light intensities or at night. It is always found with a complex of other species and becomes a fish predator within a few months after hatching. Changes in food habits as it grows are accentuated by rapid growth to large size. Larvae and fry younger than 2 mo first eat zooplankton, then mysids and gammarids. By 2–3 mo of age or 4–10 cm long, the pikeperch begins to eat fry of other fishes. It may continue feeding on mysids and gammarids up to age 2, even while feeding on young of other fishes, and especially if these invertebrates are abundant and prey fish are scarce. When pikeperch becomes predatory, its main food is mature and young schooling fishes up to 20 cm long which inhabit open water. Pikeperch often eat large numbers of their own young when they are abundant or when young of other fishes are scarce. This is characteristic of most fish predators and is regarded by Nikolsky (1950, 1960) as an adaptation for a greater utilization of the food base in a water body.

The perch, less than 50 cm long and 2 kg in weight, is less specialized. It adapts easily to life in a variety of waters, eats a wide range of foods, and uses several habitats (the vegetated littoral zone as well as benthic and pelagic areas of open water). Unlike the pikeperch, the perch grows slowly and is a facultative fish predator. Depending on conditions in a water body it feeds on littoral and benthic invertebrates and small fish, mainly young less than 12 cm long. In some waters it is the only fish species. No marine form occurs.

The perch becomes piscivorous at the same length and age as pikeperch, but complete transition to a predatory habit can be delayed by feeding conditions or slow growth. Where food is scarce perch eat plankton and benthos throughout their lives; where it is richer, they have a mixed diet; and where it is abundant, they become piscivores. Perch often form ecological groups characterized by different feeding patterns and different rates of growth and maturation in the same water body. The smallest, slow-growing animals feed on plankton until 2–3 yr of age. Larger perch, 3–4 cm long, begin eating benthos and sometimes continue eating benthos for their whole lives. Only the fastest-growing fish begin switching to a fish diet at the age of 2–3 mo and then become entirely piscivorous in autumn at lengths over 10 cm. Such differentiation occurs even within year-classes (Iljina 1970). Owing to differences in growth rate, piscivorous perch are recruited from benthic feeders regularly over time as they reach an appropriate length. In relatively stable conditions, two or three feeding groups are found in a population, but with abrupt changes in food supply one group becomes predominant. For example, increased food usually increases growth of perch and the abundance of piscivorous perch, whereas decreased food leads to slower growth and more small benthic feeders.

In some lakes in forested areas of northwest USSR, the fish fauna is represented by one species dominated by two size groups: small littoral planktivorous perch and large piscivorous perch that are cannibalistic (Menshutkin 1964, 1971). Increased abundance of medium-sized perch creates good feeding conditions for large perch, and their relative abundance increases at the expense of the slow-growing perch. When the abundance of large perch is too high, their supply of medium-sized fish is exhausted and they switch to feeding on the small planktivorous perch in the littoral zone. In this case the numbers and biomass of both small and large perch decrease because the reproductive ability of the population is reduced, i.e. fewer eggs are laid and the young-of-the-year are less abundant, which further decreases the food and, subsequently, the abundance of large perch. The lower predation pressure and less dense population create favorable conditions for survival and growth of medium-sized perch as well as the small littoral forms. Some of these then become cannibalistic and grow rapidly to repeat the cycle. Thus, increased abundance of large perch initiates a decline in small perch.

The block diagram of perch population model is given in Fig. 1. The system's state is determined by the numbers of fish in 9 age-groups N_1–N_9. The modeling of cannibalism, which is a particular case of predator–prey relationships, was based on the concepts of Shorygin (1952) and Ivlev (1961). The number of small perch (N_1–N_4) depend on the food supply (P_{pb}), while those of predator perch depend on their recruitment by plankton-feeding perch (connection through real ration = R). From the sixth year of age, perch become the object of fishing (Y = yield) with a certain intensity (F). The maximum ration (Rm) of a predator is distributed in proportion to the probability of catching its prey, and the overall effect of all predators on the prey of each age as well as other quantities are determined using appropriate formula developed by Menshutkin. Attaining maturity at 5 yr of age, all individuals have a reproductive potential (E) and deposit a certain amount of eggs (J), which at a certain level of mortality (m_j) produces recruitment in the form of the new generation (N_1).

With the help of this predator–prey model (Fig. 1) for such perch populations, a 17-yr cycle in population structure and abundance was deduced (Fig. 2). Experiments in poisoning the fauna and counting fish have validated the conclusions drawn from the model. Some of these lakes lacked entire generations owing to cannibalism (Burmakin and Zhakov 1961; Burmakin 1961; Kitaev 1964).

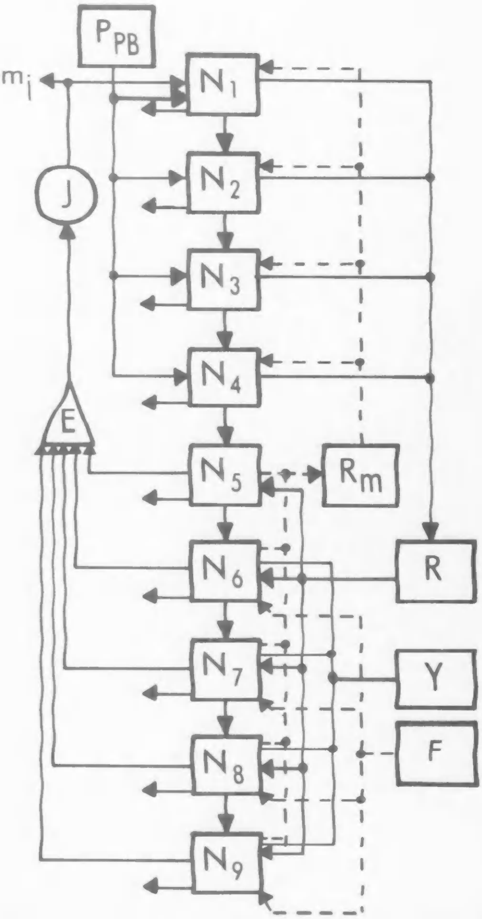

FIG. 1. Block diagram for a model of population dynamics of Eurasian perch (two forms) in Lake Tiulenye (Menshutkin 1971). (P_{PB} — food supply; $N_1 \ldots N_9$ — number in each age-group; N_1 to N_4 — planktivorous perch, N_5 to N_9 — piscivorous perch; R_m — maximum ration; R — real ration; Y — yield; F — fishing effort; E — reproductive potential of population; J — number of eggs; m_j — egg mortality). The short arrow on left side of each age-class is mortality.

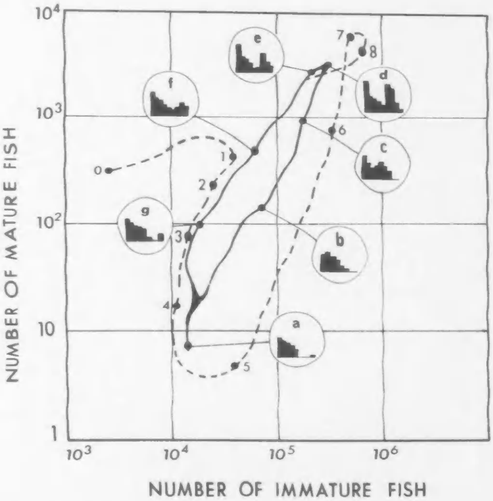

FIG 2. Phase diagram of population dynamics of perch in Tiulenye Lake (modified from Menshutkin 1971). 0, 1 . . . 8 — transition period (dotted line); solid line — repeating cycle; a–g — examples of age composition.

However, such predictable systems are rare and feeding behavior and relations of pikeperch and perch differ greatly among waters. In large lakes with abundant food and rational fishing, pikeperch and perch always become piscivorous. They grow rapidly and are abundant and important to fisheries. Young perch often fall prey to large predators such as northern pike, *Esox lucius*; pikeperch; sheatfish, *Silurus glanis*; and burbot, *Lota lota*. In shallow bodies of water with scarce food the roles of pikeperch and perch are very different. Pikeperch are still piscivorous but grow slower and are not numerous, whereas perch have a varied diet, are very abundant and have no commercial value.

Comparisons Among Water Bodies

Feeding habits of pikeperch and perch are compared below in three different water bodies at midlatitudes: the Volga delta river at 46°N and Rybinsk Reservoir and Pskov-Chudskoy Lake at 58°N. The method of calculating daily ration (Fortunatova and Popova 1973) is presented here to aid in the interpretation of the results. Fortunatova's method is based on the idea that predators eat additional prey before earlier prey are fully digested. Thus prey are in the stomach in different stages of digestion. Digestion rate of these prey in days is given in the text table below:

		Days for complete digestion	
Month	Water temp (°C)	Pikeperch, northern pike, and sheatfish	Perch
July, Aug.	>25	1	0.5
June, Sept.	18–25	2	1
May, Oct.	8–18	3	2
Apr., Oct.	4–8	4	4
Nov.–Mar.	2–4	7	7
Nov.–Mar.	0.1–2.0	9	9

A scale for the extent of digestion is also developed with five categories. This allows us to estimate how long ago the prey fish was ingested to the nearest day.

The daily ration was calculated from

$$r = \sum_{i=1}^{i=y} \frac{S_i \div n_i}{V} \cdot \frac{n}{N}$$

where, r = daily ration in percentage of the predator's weight
V = number of days for complete digestion
N = number of predatory fish sampled
n = number of predatory fish in sample that contained food
n_i = number of predatory fish that fed on each of the preceeding V days
S_i = the quantity of food eaten by the predators on each of the preceeding V days expressed as a percentage of the predator's weight.

If digestion time was 1 day the formula simplifies to $r = S/N$. An example calculation (Fortunatova and Popova 1973) is presented here for clarification. In May at 8–18°C digestion was complete in 3 days ($V = 3$). Of the 30 predators in the sample ($N = 30$), 20 contained food ($n = 20$). Examination of the food in the stomach indicated that 10 predators contained food eaten on the day of capture, or at stage I of digestion ($n_1 = 10$, $S_1 = 13.5$); 15 predators contained food eaten the day before or stage II of digestion ($n_2 = 15$, $S_2 = 19.5$); and 7 predators contained food eaten 2 days earlier in the stages of digestion III–V ($n_3 = 7$, $S_3 = 15.35$). By the formula, we obtain

$$r = \left(\frac{\frac{13.5}{10} + \frac{19.5}{15} + \frac{15.35}{7}}{3}\right)\left(\frac{20}{30}\right)$$

$$= 1.07\% \text{ body wt/day.}$$

Volga delta (Fortunatova and Popova 1973) — In the Volga delta, a complex of shallow water bodies, ecological conditions are favorable for spawning, feeding, and growth of both species. The ecosystem contains piscivorous fishes (pikeperch; sheatfish; northern pike; asp, *Aspius aspius*; perch; and Volga pikeperch), 25 fishes that eat benthos, and 15 planktivorous fishes. The predominant planktivores are 17 cyprinids, 9 gobies, 4 clupeids, 4 acipenserids, and 4 percids. Food of piscivorous perch and pikeperch consists mostly of small cyprinids and gobies, which form large concentrations while spawning, and young of these species during the growing season.

The annual feeding cycles of pikeperch and perch are tied closely to seasonal changes in the abundance of their food supplies. In addition, differences in behavior, habitat, and size of perch and pikeperch alter the availability of food organisms as well as their choices of food and annual rhythms of feeding.

Pikeperch feed most heavily in April–May (Table 1, Fig. 3) on spawning Caspian roach, *Rutilus rutilus caspicus* (Fig. 4, 5) to obtain up to 80% of their annual ration. A second peak in feeding (Table 1, Fig. 4) occurs on prewinter concentrations of young roach (Fig. 4) and other species. Roach are generally too large for perch to eat. In spring and summer perch eat mostly young cyprinids and spawning gobies. To a lesser extent they also feed on prewinter concentrations of the same species. Composition of the diet and intensity of feeding vary somewhat with limnological conditions in each year, but the general features of feeding by both predators remain the same.

Rybinsk Reservoir (Ivanova 1965, 1968) — The fish fauna of Rybinsk Reservoir is less diverse than that of the Volga delta with only 25 species. Acipenserids, clupeids, gobies are absent, and representatives of a boreal arctic complex appear: small smelt, *Osmerus eperlanus eperlanus*; or stint, *O. e. spirinchus*; and burbot, which replaces sheatfish. The food supply of the predators consists mainly of roach, *Rutilus rutilus*; ruffe; young perch; and stint concentrated to spawn and feed.

In low-water years pikeperch feed most heavily in spring on spawning roach and in summer on young perch. In high-water years the main feeding occurs in spring on spawning concentrations of stint and roach and in autumn on ruffe and young perch. Perch are in as good condition as in the Volga delta, but, even though pikeperch prefer roach and ruffe, the main food of perch consists of its own young.

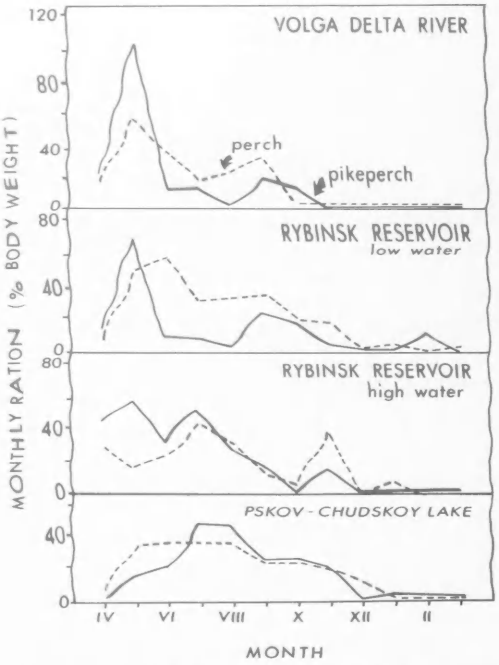

FIG. 3. Annual cycle of feeding intensity for pikeperch and perch in Volga delta river, in Rybinsk Reservoir at low water levels in 1960 and high water levels in 1961, and in Pskov-Chudskoy Lake. Modified from fig. 35 in Fortunatova and Popova (1973), Ivanova (1965, 1968a, b), and Pihu and Pihu (1974).

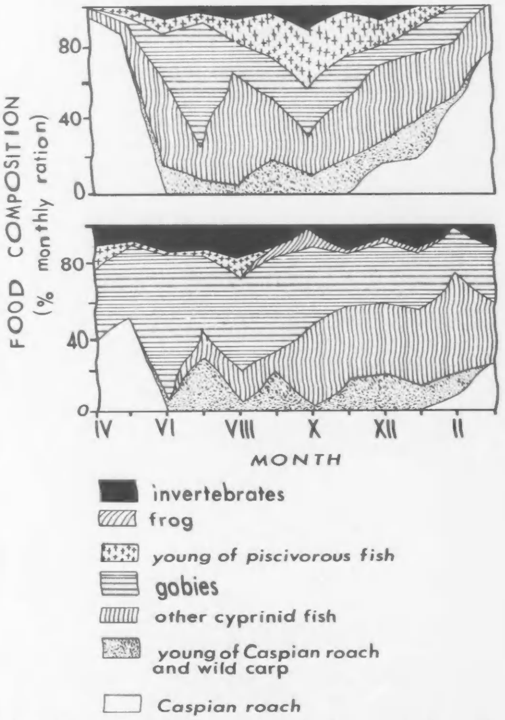

FIG. 4. Seasonal changes in food composition of pikeperch (above) and perch (below) in the advanced edge of the Volga river delta in 1953 (modified and expanded from fig. 41 in Fortunatova and Popova (1973).

Pskov-Chudskoy Lakes (Pihu and Pihu 1974) — In Pskov-Chudskoy Lake the composition of the fish fauna is similar to that in Rybinsk Reservoir. Additional species here are coregonids (vendace, *Coregonus albula*, and whitefish, *Coregonus lavaretus*), which supplement the food base of the predators, and the eel.

The composition of the diet and feeding cycles of pikeperch differ more from perch here than was the case in the Volga delta and Rybinsk Reservoir (Fig. 3, 5). In all seasons the main food of predators is stint, which is high in abundance. The heaviest feeding of perch occurs in spring, on spawning stint, and in summer, on growing stint and ruffe. The main feeding of pikeperch occurs in summer, on growing stint. Both species eat vendace but not in great quantity. In years when stint are declining sharply in abundance (1972–74), they are absent from the diet of predators. In such years the main food consists of ruffe and young perch in summer and autumn and, to a smaller extent, roach in spring. In these years the pattern is similar to that of the Rybinsk Reservoir, with the diet of pikeperch being dominated by ruffe and that of perch by its own young.

Karelia Lakes (Kudersky 1961a, 1962) — Farther north, in Karelia Lakes (Sjam Lake) vendace is more important to pikeperch and perch than in the lakes above. It sometimes becomes the main food of predators in the summer and autumn (Fig. 4).

Comparisons concerning latitude — In general, at the midlatitudes (50–60°N) typical foods of the two species are roach, ruffe, and perch (Fig. 5). These are replaced by smelt and vendace in the north and gobiid fish in the south.

Increases in the duration of the feeding period from north to south correlate both with increases in growth rate of pikeperch and perch and with decreases in age of sexual maturity and life span (Popova 1971; Novokshonov 1974; Tanasiychuk 1974) (Table 2). We observed that digestion

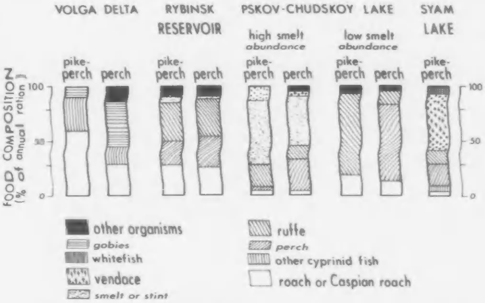

FIG. 5. Food composition of pikeperch and perch in % of annual ration for four waters of the USSR including one with high and low smelt abundance. Source: Volga delta (Fortunatova and Popova 1973), Rybinsk Reservoir (Ivanova 1965, 1968a, b), Pskov-Chudskoy Lake (Pihu and Pihu 1974), and Syam Lake (Balagurova 1963).

rate, active feeding and intensive digestion began in pikeperch and perch at 8–10°C. These temperatures were exceeded in the waters of the Caspian, Aral, and Azov basins for 6–7 mo, in the midlatitude for 5.5 mo, and in Karelian waters for only 4–4.5 mo.

The slowest growth rate and oldest age at maturity are observed at the northern and southern edges of their ranges. In the north, not only does the short growing season contribute to this, but also cool water temperatures and scarce food supplies. Predators in the north continue feeding in winter. But, even with continued feeding, at a water temperature below 8°C fatness and condition remain the same as in the growing season (Lapitsky 1970). In waters in the extreme south of Middle Asia the long growing season does not correspond to a long period of intensive feeding, because water temperatures exceed 25°C. According to our observations feeding activity falls at these high temperatures, and, even though digestion rate is high, intervals between meals are long. The food supply of the pikeperch and perch in these waters is unusual and consists of lithophils of the front-Asian complex. All of these factors contribute to slow growth rate and low fecundity.

Variations in annual rations — The annual ration is more variable from year to year in Rybinsk Reservoir and Pskov-Chudskoy Lake than in the Volga delta. In the Volga delta, where intensive feeding continues for 7.5 months, the annual ration of an adult pikeperch is equivalent to 200–220% of body weight; that of perch, 175–220%. Food supply is high and varies little among years, because both abundance and availability of their principal prey are high. But in the Rybinsk Reservoir and Pskov-Chudskoy Lake the growing season is shorter (5.5 mo), and feeding continues under the ice. Depending on feeding conditions in these two lakes, annual ration of pikeperch varies from 180 to 250% of body weight, and that of perch from 185 to 275%. An important role is played by short-lived species such as smelt, which vary considerably in abundance owing to temperature fluctuations in different years (Tjurin 1974; Popova 1975). In addition, fluctuations in water supply in different years result in different numbers of young perch, ruffe, and roach. Consequently, annual ration and the feeding cycle in these waters differ considerably between years.

TABLE 1. Daily rations of perch and pikeperch in 1953 averaged by month for the Volga delta in % of body weight.

	Apr.	May	June	July	Aug.	Sept.	Oct.
Perch	—	3.90	2.30	0.66	0.82	1.14	0.10
Pikeperch	1.77	4.11	0.53	0.50	0.35	0.86	2.39

Annual rations of pikeperch for the years 1948, 1949, and 1953 in the Volga delta river and in the Rybinsk reservoir varied only from 200–250% of body weight per year. In 1953 the annual ration was the largest — in 5 summer mo the pikeperch ate 220% of body weight and the perch 230%. Since winter feeding is about 20% of the annual ration, the annual ration of these predators in 1953 would have been about 300% body weight. This is a fairly large ration, especially because most of it is taken in May–June and October. In addition, the prey have a higher caloric value than the predator: ca 1.8 cal/g for prey fish vs. 0.8 cal/g for predators.

We observed that the annual ration of species varies over a specific range depending on feeding conditions. Maximum annual ration may be 2–3 times the minimum. Thus, feeding conditions for a species in a year can be judged by the annual ration. Additional published data on annual food consumption are scarce (Biro 1969), but results are similar to ours. When annual ration equals 200% of the body weight (close to the maximum), the pikeperch population has had good feeding conditions, and, with rational fishing and high abundance, such populations can be expected to be highly productive, e.g. the stocks in the Volga delta in 1940–55 (Fortunatova and Popova 1973), in Vyrtsjarv Lake (Pihu 1975), and in Kurshsky Bay (Gerulaitis 1972; Virbickas et al. 1974). When the annual ration falls to a lower limit of 70–80% of the body weight, the pikeperch is short of food, grows slowly, and

TABLE 2. Latitudinal differences in average lengths (cm) and weights (g) of pikeperch of various ages in USSR waters (modified from Novokshonov 1974).

	Northern latitudes (≥60°N)		Mid-latitudes (50°–60°N)		Southern latitudes (≤ 50°)	
Age	Length	Weight	Length	Weight	Length	Weight
1	12	38	12	31	18	73
2	16	99	24	231	31	392
3	22	176	32	488	39	754
4	26	260	41	864	45	1,236
5	32	429	47	1,401	51	2,534
6	36	621	52	1,832	57	2,534
7	40	882	58	2,472	64	3,805
8	44	1,204	62	3,242		
9	48	1,555	67	4,386		
10	51	1,916				
11	53	2,024				
12	56	2,500				
13	58	3,468				
14	58	2,720				
15	64	3,408				
16	61	3,316				

is subject to mass mortality. Pikeperch of Balaton Lake provide an example of such conditions (Biro 1969).

Differences in availability of prey for young and mature predators produce differences in the cycles of the predators' food habits and habitat occupation. Thus, in the Volga delta adults (Fortunatova and Popova 1973) prefer the lower reaches, where they feed, mainly in spring, on spawning Caspian roach (in the case of pikeperch) and in summer on spawning concentrations of gobies (in the case of perch). As the young migrate downstream in summer to the lower part of the delta, they feed in the middle zone of the delta on young cyprinids. Young pikeperch feed during summer in the shallow zone of the Caspian Sea at the edge of the delta on kilka, *Clupeonella delicatula*, and in the underwater delta on gobiid fishes (*Neogobius*, *Caspiosoma*, *Benthophilus*, *Pomatoschistus*, *Mesogobius* spp.) (Fig. 6).

Intensity of feeding also changes with age. Thus, in the Volga delta (Fortunatova and Popova 1973) a 1–2-year-old pikeperch consumes as much as 264% of its body weight in a year, whereas a 3–4-year-old fish consumes 224% and a 5–6-year-old 157%.

Interactions Among Species

The above observations suggest that in spite of a considerable overlap in feeding habits of pikeperch and perch, competition for specific foods is markedly reduced, because these predators occupy different habitats and prefer different foods. In addition, competition is reduced by differences in times of intensive feeding and by consumption of prey of different sizes. Each species has developed adaptations that reduce competition in intraspecific food relationships (Nikolsky 1953b; Kudersky 1961a; Popova 1965, 1967, 1971). These include differences in feeding areas, spectra of food, size of prey and feeding cycles of the different age-groups; formation of ecological forms that occupy new niches and develop new food habits (i.e. perch); regulation of abundance by cannibalism when food supply is low; and decreases in growth rate, age at maturity, and fecundity.

With our method for determining daily, monthly, and annual rations of predators (Fortunatova and Popova 1973; Manual 1974) we can determine the total quantity of food consumed in a year by one fish or by the whole population, as well as the predation pressure on a prey species. If the ration, the composition of the diet, and mean weight of each prey species are known, the number and weight of each species eaten by the predator (Table 3) can be calculated. From the total catch of a predator, the mean weight of a predator, and its annual ration, the number and biomass of prey removed from the water body by the predator (Table 4) can also be calculated. (Table 4 is an example of an estimate of biomass and numbers of Caspian roach withdrawn from the Volga delta by the entire complex of predacious fish.)

In 1950–55, the Volga delta fishery took 60.8 thousand tons of Caspian roach, or 500 million individuals averaging 18 cm long and 2–3 yr old. The complex of predatory fish took 52.67 thousand tons (Table 4), or 1470 million Caspian

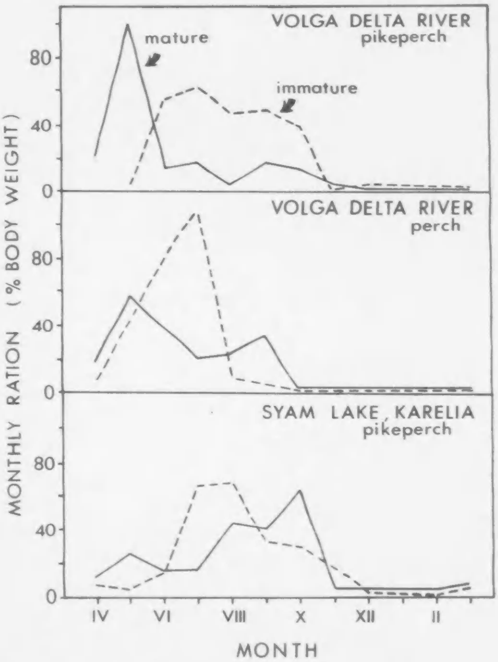

FIG. 6. Annual cycle of feeding intensity by mature and immature pikeperch and perch in different water bodies. Modified from fig. 35 in Fortunatova and Popova (1973) and Kudersky (1962).

roach averaging 12 cm long and 1–2 yr old. Of the total eaten, 20% was consumed by pikeperch and only 5% by perch. The catch of each predator was assumed to be about one third of the standing stock of the predator population and, thus, approximately equal to the weight of predators (young adults) that prey significantly on mature or commercial Caspian roach. By also accounting for consumption of young Caspian roach by immature predatory fish, we estimate that all predatory fishes in the delta annually eat about 10 billion Caspian roach, or 12% of each year-class or 22% by weight and 24% by number of the entire Caspian roach population. In addition, all predatory fishes annually eat about 30 billion small forage fishes, about 2.5 billion young predatory fish, and up to 1 billion frogs, which totals 50.4 thousand tons.

As the predator grows, certain food items are replaced by other, larger food items (Table 5). As the width of the mouth and the stomach size increase as the fish grows, the range of available prey increases but the average length of prey changes only slightly. Both species prefer fish 8–12 cm long (Fig. 7). These prey are easiest to catch and are more rapidly digested and assimilated. Our observations have shown that pikeperch and perch feed mainly on immature individuals (ruffe, perch, and young cyprinids). When a prey species is abundant, adults are also eaten (Caspian roach, smelt, vendace, and gobiids). These adults are usually the smallest slow-growing fish, the sick, and specimens weakened after spawning, mostly males. Thus predators affect the populations of their prey differently than would a fishery which takes mature fish including the largest and fattest specimens (Fortunatova 1957, 1961; Popova 1967; Fortunatova and Popova 1973; Nikolsky 1974).

TABLE 3. Numbers of organisms of various groups consumed by single immature and mature pikeperch and perch during a year in Volga delta (modified from Fortunatova and Popova 1973).

	Commercial species		Noncommercial species		
Predator	Caspian roach	Young cyprinids	Small forage fish	Young predatory fish	Frogs
Pikeperch					
immature	15	39	300	5	—
mature	48	112	218	55	6
Perch					
immature	—	212	125	5	—
mature	4	85	52	11	1

In any estimation of the role of predatory fish in a water body, we emphasize that predators tend to stabilize the community by consuming the most abundant species and thus balancing all the links of the food chain. Predators easily switch to another prey if abundance of their main food falls below a certain level. Thus, even the consumption of a large number of commercial fish by predators cannot be regarded as detrimental to a fishery because reducing their abundance improves the feeding conditions and the growth rate of the survivors. By usually consuming the weakest members of commercial fish populations and by removing small forage fish which compete with commercial fish, predators act as biological meliorators. They also convert low value fish into products of a superior quality. Pikeperch and perch have higher conversion rates than other predators in the Volga delta on a wet weight basis — pikeperch (19.6%), perch (18.2%), sheatfish (16.1%), asp (16.1%), and northern pike (11.4%) (computed from Table 77 in Fortunatova and Popova 1973).

A decrease in predators by overfishing inevitably leads to a sudden rise in the abundance of small coarse fish (roach, ruffe, small-sized

TABLE 4. Calculation of weight and numbers of mature Caspian roach eaten per year by predacious fish in the Volga delta from 1950 to 1955 (modified from table 74 in Fortunatova and Popova 1973).

Values	Predators					
	Sheatfish	Northern pike	Pikeperch	Asp	Perch	Total
A. Catch[a] tons × 10^3 (Number × 10^6)	7.9 (2.8)	6.4 (4.0)	28.5 (14.2)	1.3 (1.3)	5.95 (9.8)	50.05 (32.1)
B. Annual ration (% body weight)	200	340	220	170	230[b]	—
C. Weight of all fish eaten $= \frac{A \times B}{100}$ (1,000 tons)	15.80	21.76	62.70	2.21	13.68	116.15
D. Caspian roach in annual ration (%)	50.0	27.0	57.0	2.3	22.0	—
E. Total Caspian roach eaten $= \frac{C \times D}{100}$ tons × 10^3 (Number × 10^6)	7.90 (160)	5.87 (235)	35.74 (966)	0.05 (2)	3.01 (107)	52.67 (1470)

[a] Catch is about one-third of the predator stock and approximately equal to the weight of the young adults that feed on mature Caspian roach.

[b] Quantity eaten from June to October only.

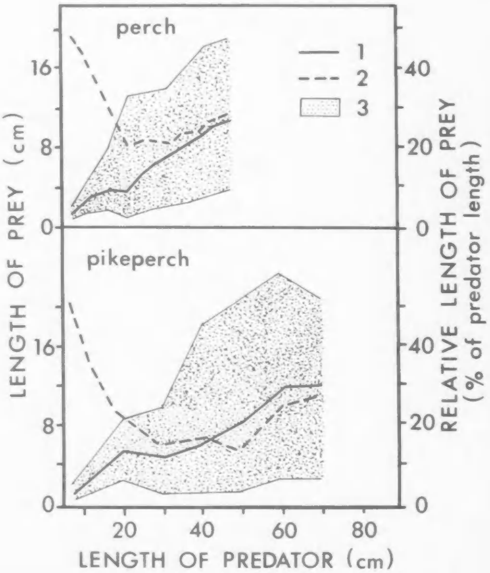

FIG. 7. Relation between length of predator and length of prey in Volga delta river. 1, average length of prey; 2, relative length of prey; 3, range in length of prey. Modified from fig. 33 in Fortunatova and Popova (1973).

perch), which use the entire water body and suppress or displace more valuable species. According to Elton (1933), if the density of a population is too low, it can easily go extinct.

TABLE 5. Food composition (% by weight) of pikeperch in Syam Lake as influenced by the length of the predator (modified from Kudersky 1961a).

Prey	Length of predator(cm)							
	5	10	15	20	25	30	40	50
Vendace	2	7	21	40	47	44	54	
Whitefish	—	—	—	—	—	—	7	
Ruffe	14	76	60	41	44	44	16	
Young pikeperch and perch	8	9	15	19	6	6	14	
Cyprinid fishes	—	2	2	—	—	6	6	
Invertebrates	76	6	2	—	3	—	3	

Tyurin (1973, 1974) proposed that every species has a critical threshold of abundance above which abrupt increase in abundance occurs and below which further depression occurs. Overfishing the predators to levels below this threshold leads to depression of their populations (as with pikeperch in Pskov-Chudskoy Lake) and to explosive increases in small forage fish. Control of the latter can be achieved only by biological methods, i.e. with a sufficient increase of predatory pressure. Restoring the abundance of predators, if their own reproduction is insufficient, is possible only with the help of man through a complex of measures to limit the catch and supplement natural reproduction.

The roles of pikeperch and perch are different. The pikeperch is always a predator, occupies the top position in food webs, and is a valuable commercial object, whereas the perch in most lakes occupies an intermediate position in food webs and is prey for larger predators. Thus the role of pikeperch is usually biomeliorative and the predatory form of perch also plays a meliorative role. But slower-growing perch are useless and require steady and intense predation pressure from piscivores. Usually the abundances of pikeperch and perch are inversely related (Svärdson and Molin 1973).

In view of valuable characteristics of pikeperch such as rapid growth, broad food habits, high conversion rate of food, and palatability to man, it is often used to enrich the fish fauna and control small fish of little value. The measure is usually successful only in water bodies with relatively good food supplies (Gladky 1973). In some waters of Middle Asia with a poor fish fauna the pikeperch annihilated populations of local species which had no adaptations to counter such high predation pressure. Initially pikeperch grew quickly and reproduced but later, due to absence of other food, it became cannibalistic and even ate zooplankton. Then the growth rate and abundance declined sharply (Dikansky 1974; Strelnikov and Dikansky 1975). Therefore, when introducing pikeperch as a fishery management measure, special attention should be given to the food supply at all stages of development of pikeperch. This may necessitate additional introduction of invertebrates like mysids and gammarids or fish like smelt or gobies.

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Factors Affecting the Shift in Predominance from Eurasian Perch (*Perca fluviatilis*) to Roach (*Rutilus rutilus*) in the Kličava Reservoir, Czechoslovakia[1]

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Pivnička, K., and M. Švátora. 1977. Factors affecting the shift in predominance from Eurasian perch (*Perca fluviatilis*) to roach (*Rutilus rutilus*) in the Kličava Reservoir, Czechoslovakia. J. Fish. Res. Board Can. 34: 1571–1575.

A shift in predominance from Eurasian perch (*Perca fluviatilis*) to roach (*Rutilus rutilus*) in the Kličava Reservoir in 1964, 10 yr after filling, was attributed mainly to a marked decline in the ratio of female to male perch spawners. The ratio was about 1:4 for perch and unity for roach. Fecundity of perch was about 25% that of roach which, together with the decline in spawning females, probably contributed to smaller year-classes. The decline in growth rate of perch in response to increasing abundance was greater than that for roach. Under equal environmental conditions, roach is also more productive than perch.

Key words: Percidae, *Perca*, *Rutilus*, Kličava Reservoir, Czechoslovakia, shift in predominance, fecundity, sex ratio, methodology, growth–abundance relationships

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Un déplacement de la prédominance de la perche eurasienne (*Perca fluviatilis*) en faveur du gardon (*Rutilus rutilus*) dans le réservoir de Kličava en 1964, 10 ans après remplissage, est attribuable surtout à un déclin marqué des perches femelles par rapport aux mâles reproducteurs. Ce rapport est d'environ 1:4 pour la perche et proche de l'unité pour le gardon. La fécondité de la perche est d'environ 25% de celle du gardon, ce qui, avec le déclin des femelles reproductrices, contribue probablement à de plus petites classes d'âge. Le déclin du rythme de croissance de la perche en réponse à une plus grande abondance est plus prononcé chez le gardon. Dans des conditions ambiantes identiques, le gardon est en outre plus productif que la perche.

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This is a report on the factors considered responsible for a shift in predominance from Eurasian perch (*Perca fluviatilis*) to roach (*Rutilus rutilus*) in the Kličava Reservoir 10 yr after filling. Data are provided for sex ratios at spawning, growth, and abundance for two periods after filling, 1963–64 and 1967–72.

The Kličava Reservoir in Central Bohemia, Czechoslovakia, was filled in 1954–55 to supply water to the town of Kladno. The average surface area is 60 ha, the maximum depth 37 m, and the mean volume 9.5×10^6 m^3. As the afferent brooks are equipped with wire sieves, migration of fish into and out of the reservoir is not possible under normal conditions (Holčik 1970). Fishing in the reservoir is forbidden.

Before the dam was built the Kličava brook contained the following species: *Lampetra planeri*, *Salmo trutta m. fario*, *Phoxinus phoxinus*, *Noemacheilus barbatulus*, *Perca fluviatilis*, and *Cottus gobio* (Oliva 1949). Other species (*Cyprinus carpio*, *Leuciscus cephalus*, *Rutilus rutilus*, *Scardinius erythrophthalmus*) were probably washed into the reservoir during flooding of ponds situated higher in the drainage area. In 1957, perch accounted for 88% of total numbers and 57% of fish biomass (Holčik and Pivnička 1972). The population, estimated at 59,400 by the Schnabel method (Oliva and Holčik 1965) declined to 20,000 in 1964 and to 10,000 in 1967 and 1972. In 1964, roach became predominant and between 1964 and 1970 accounted for 75–86% of numbers and 70–85% of the biomass of the entire fish stock of the reservoir. Abundance of age 3 and older roach increased from 20,000 in 1964 to 100,000 in 1967.

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TABLE 1. Abundance of perch in the Kličava reservoir in 1963, 1964, and 1967–72, kilograms of total production (P) and available production (P_A). Underlined figures are estimated values. Arrows indicate direction of calculations.

Age-group	1963	1964	1967	1968	1969	1970	1971	1972
1	16400	$\underline{23750}$	50003	35163	22390	14543	$\underline{830}$	$\underline{15000}$
2	4485	$\underline{4920}$	4851	15001	10549	6717	4363	515↓
3	9581	$\underline{2570}$	$\underline{3450}$	$\underline{2780}$	8596	6045	3849	2500↓
4	5322	$\underline{5490}$	$\underline{2330}$	$\underline{2565}$	1593	4926	3464	2206↓
5	3577	$\underline{3050}$	$\underline{350}$	$\underline{790}$	1470	901	2823	1985↓
6	2129	$\underline{2050}$	$\underline{90}$	$\underline{180}$	453	852	$\underline{320}$	1618↓
7	820	$\underline{1220}$	$\underline{32}$	$\underline{120}$	103	260	$\underline{80}$	174↓
8	—	$\underline{470}$	$\underline{122}$	$\underline{10}$	69	59	$\underline{149}$	147↓
Total	42314	43520	61228	56609	45223	34293	15878	24145
P(2nd–8th age-group)	696.2	719.2	343.8	483.4	—	434.8	376.5	268.1
P_A(1st–8th age-group)	633.6	753.5	618.2	633.8	—	465.7	302.5	397.0

TABLE 2. Abbreviations and equations used in text.

P^t_A available production at the time t	$P^t_A = \sum_{i=1}^{n} A^t_i W^t_i$
P^t total production	$P^t = \sum_{i=2}^{n} G^t_i \bar{B}^{-t}_i$
$P^t_{I(i)}$ index of production of ith age-group	$P^t_{I(i)} = \sum_{i=2}^{i} G^t_i \bar{B}^{-t}_i, A^t_i = 1$
G^t_i instantaneous growth coefficient	$G^t_i = \log_e w^t_i - \log_e w^{t-1}_i$
W^t_i absolute weight increment	$W^t_i = W^t_i - W^{t-1}_i$
B^t_i, $\bar{B}^{-t}_i$, biomass, mean biomass	$B^t_i = A^t_i W^t_i$, $\bar{B}^{-t}_i = \frac{B^{t-1}_i + B^t_i}{2}$
A^t_i abundance, N^t abundance of all age-groups	$N^t = \sum_{i=1}^{n} A^t_i$
i 1, 2, 3, ... $n - 1$, n age-groups	
t 1, 2, 3, ... $i - 1$, i years of life of the ith age-group	

Methods

Schnabel's method was used to estimate the abundance (Table 1) of perch in 1964 (Holčik 1969), 1967, 1968, 1971, and 1972 (Pivnička 1971; Černý and Pivnička 1973; K. Pivnička unpublished data). For 1963, 1969, and 1970 the abundance was calculated from age composition data using the mean value of survival rate,

$$S = 0.573\left(S = \sum_{i=4}^{8} A_i^{1968} \Big/ \sum_{i=3}^{8} A_i^{1967} = 3665/6374 = 0.573\right).$$

Abbreviations and equations are summarized in Table 2.

The following survival rates were calculated from the numbers in the successive age-groups of perch samples: 1964 — 0.463; 1967 — 0.577; 1968 — 0.624; 1970 — 0.419; 1971 — 0.717; 1972 — 0.562 ($\bar{X}$ = 0.560). These rates were used for the 2–8-year-old fish. A survival rate of S = 0.3 was presumed for the 1–2-yr-old fish. This value was supported first by the mean value of 0.223 calculated from the samples in the years 1963, 1964, 1972, and 1973 (the individual values being 0.364, 0.208, 0.034, and 0.286, respectively) and second by the regression calculated from age-group 4 in 1967 (2330 ÷ 0.573 ÷ 0.573 ÷ 0.3 = 23,655). Holčik (1970) estimated 23,750 perch for age-group 1 in 1964. The essential point was that all derived estimates divided into age-groups using "S" had to agree with the percentile representations of the age-groups in samples. This enabled an estimate of even younger age-groups which had not been caught proportionately in the gill and fyke nets (for roach and perch, respectively).

Weights were calculated from the log–log relationship between body length (mm) and weight (g). The log *w* values for the two periods were:

Year	Value	Source
1963(359)[a]	3.1520	Holčik (1969)
1964(1147)	3.1766	Holčik (1969)
1967(510)	3.1134	Pivnička (1971)
1968(431)	2.9921	Pivnička (1971)
1970(287)	3.0041	Pivnička (1971)
1971(149)	2.9633	Švátora (1973)
1972(331)	3.1514	Švátora (1973)

[a]Number of fish examined.

Growth in individual age-groups was calculated as an index of production $P_{I(t)}$. This value comprised partial values, which, in essence, represented the weight increments but were calculated as the production made by the particular age-group during its lifetime. In practice, the first partial value of $P_{I(t)}$ was calculated beginning with the second year of life of each age-group. In the first age-group, the weight value was employed instead of the value of $P_{I(t)}$.

Our evaluation of the sex ratio at spawning sites was based on the assumption that the male to female ratio in the perch population is unity except for the oldest individuals (Pivnička 1972). This was demonstrated in 1967 in the Lipno Reservoir, where the percentage of females at spawning sites just before spawning (April 1–15) was 50.4 and declined to 9.2 during spawning (April 27–May 2). If sexually immature and unripe females are excluded from the prespawning sample the percentage of potential female spawners is reduced to 8.5 which agrees closely with the 9.2% found during spawning.

The logarithmic equation ($y = a - b \log_e x$) was used to calculate relationships between abundance and each of fecundity, growth, production, and female proportion in the population (Backiel and Le Cren 1967).

Data on female perch longer than 160 mm were excluded from the abundance–fecundity equation for the following reasons: (a) an occasional large female with a high rate of fecundity occurring incidentally in any year can change the average fecundity for that year (material for the study of fecundity is limited) and; (b) in comparison with the remaining fishes of the population these large females behave mainly in their feeding habits as a "different species" and impede considerably the assessment of data on the relationship between fecundity and amount of food available (the latter being dependent on the number of fishes present). The size limitation in the roach data is due mainly to the limited number of females available for the fecundity study. However, the size-group of 180–200 mm was representative because it was the largest group in the roach spawners in all years.

Growth–abundance relationships for perch were calculated from several values obtained in the years 1967–68 and 1970–72 except that data from 1963 and 1964 were added for age-groups 1 and 8. In all other calculations these values were not used because they were outside the general course of the growth abundance curves.

For the relationship between production and abundance, the data from 1963 and 1964 also diverge from the general trend and have not been used in calculating the equations.

The calculation of maximum theoretical values of abundance and production per hectare was based on the equation of the production–abundance relationship ($y = x(a - b \log_e x)$). The first derivation of this equation was taken to zero. It was then possible to calculate directly the maximum theoretical value of abundance and the corresponding value of production: $y = x(a - b \log_e x)$; $y^1 = a - b \log_e x - b$; $a - b \log_e x - b = 0$; $\log_e x = a - b/b$.

Sex Ratios in Spawning Shoals and Fecundity

The ratio of female to male spawners was usually less than 1:4 for perch and unity for roach (Table 3). The percentage of female perch spawning in the Kličava Reservoir was low during the entire spawning period. Numbers of perch sampled and percentages of females in 1968 were:

	April		May		
	18	24	1	7	14
Number	35	618	1222	1550	567
%	0	6	10.5	7.4	9.3

Numbers of female perch were highest in those years when perch abundance was lowest. The relationship is shown by the equation $y = 10.9 - 1.9757 \log_e x$ ($r = -0.513$). The number of females in the spawning shoals is influenced by age composition as well as abundance. In years when older age-groups are predominant the number of spawning females increases and vice-versa. This occurs because only males are sexually mature in age-group 1 and their mortality rate is higher (the oldest perch are always female).

The absence of immature and unripe females at spawning sites, rather than increased activity of males might explain the low percentage of females during spawning. The percentage of females in spawning shoals in the Lipno Reservoir averaged only 6.7 for the years 1965 to 1968. Alm (1946) described a similar situation for Swedish lakes where the percentage of female perch was low during spawning, but the post-spawning sex ratio was almost unity. The majority of females do not spawn each year and in the Kličava Reservoir this behavior may be associated with the availability of food. On the other hand the ratio of female to male roach during spawning

TABLE 3. Estimated numbers of perch (N), percentages of female perch, absolute numbers of female perch in age-classes 2–8 (NF), numbers of perch sampled (*n*), and percentages of female roach in Kličava reservoir.

	1964	1967	1968	1969	1970	1971	1972	1973	1974
					Perch				
N	42314	61228	56609	45223	34293	15878	24145	—	—
%	12	11.2	8.3	19.1	25.1	37.5	12.6	13.8	11.6
NF	2360	1270	1780	4400	4950	5620	1150	—	—
n	5031[a]	1872	3995	831	427	231	331	236	126
					Roach				
%	—	44	51	65	39	57	57	50	68

[a] Holčik (1969).

TABLE 4. Values of coefficients *a* and *b* of growth–abundance relationships of perch in Kličava reservoir and correlation coefficients *r* (0.8 and higher are significant at $P = 0.05$).

Age-group	*a*	*b*	*r*
1	12.901	−0.853	−0.146
2	58.782	−4.692	−0.926
3	75.825	−4.922	−0.303
4	148.734	−12.281	−0.546
5	6.012	+8.733	+0.667
6	186.729	−18.693	−0.865
7	571.945	−93.244	−0.843
8	481.400	−44.655	−0.164

is almost unity (54% female for the 1967–74 period).

The decrease in the number of spawning females in an increasing population of perch is followed by a decrease in fecundity of spawning females. This relationship may be expressed by the equation $y = 16.71 - 2.4178 \log_e x$ ($r = -0.663$) for females up to a body length of 160 mm. For roach the relationship of fecundity of females (180–200 mm) and abundance (age 4 and older) is expressed by the equation $y = 55.72 - 4.9551 \log_e x$ ($r = -0.856$). Although there is a decrease in fecundity in an increasing population of roach, the decline is not as great as that of perch in view of its relatively low fecundity (perch fecundity is about 25% of that of roach). The equations indicate that an increase in abundance from 10 000 to 50,000 individuals is associated with a decrease in fecundity of 35% in perch and 20% in roach.

Both the low numbers of spawning female perch and their fecundity result in the release of fewer eggs. However, the simple conclusion that fewer eggs result in a smaller year class is complicated by factors influencing the rate of fry mortality (temperature, food availability, predation, etc). Menshutkin et al. (1968) considered that the mortality of perch fry might range from 1 to 100% under different conditions of water temperature and food. However, the reduction in the abundance of perch in the Kličava Reservoir can be interpreted as an indication of a positive relationship between abundance of adults and number of fry (Nikolsky 1965).

Growth and Production

The coefficients *a* and *b* of the growth–abundance relationship and corresponding correlation coefficients are given in Table 4. Common to both species is the ascending trend of the slope in the growth-abundance curves in relation to age. For age-group 3 the values of *b* were similar for perch (−4.9220) and roach (−4.4190) but for the older fish *b* is two or three times higher for perch. In our opinion this phenomenon is related to the difference in diet of the two species according to age and to their different gross efficiency of food utilization. The young of the two species appear to share common food and have the same food utilization while for older perch food density in the Kličava Reservoir is lower than that for roach and efficiency of food utilization is probably also lower. Therefore a small increase in the abundance of perch is followed by a considerable decrease in growth.

The curve representing the relationship between production and abundance in Kličava Reservoir is similar to the theoretical curve (Ivlev 1947) but the shape of the curve is variable for different age-groups (Table 5). The observed maximum values of production and abundance of roach (Table 5) are far from the expected values, especially when total production is calculated for age-groups 2–8. Maximum observed values attain only 6.1 and 1.1% of expected ones. Even if the total production of age-groups 4–8 is calculated, the maximum observed values of production and abundance are less than expected. On the other hand, the expected values of

TABLE 5. Expected and observed maximum values of total production (P, kg ha^{-1}) and abundance (N ha^{-1}) of perch and roach in Kličava reservoir for age-groups 2–8, 3–8, and 4–8.

	Perch			Roach		
	Exp.	Obs.	$\frac{o}{e}100$	Exp.	Obs.	$\frac{o}{e}100$
			Age-classes 2–8			
P	10.33	7.22	69.9	1183.26	71.8	6.1
N	1014	320	31.6	154800	1626	1.1
P =	N(0.08072–0.01019 $\log_e$N)					
r	−0.9482			−0.4190		
			Age-classes 3–8			
P	4.44	3.76	84.7	52.78	67.96	128.8
N	363	195	53.7	2430	1607	66.1
P =	N(0.08424–0.01222 $\log_e$N)					
r	−0.4996			−0.5634		
			Age-classes 4–8			
P	2.13	2.59	121.6	28.04	26.93	96
N	79	104	131.6	1258	870	69.2
P =	N(0.14541–0.02709 $\log_e$N)					
r	−0.7313			−0.8323		

production and abundance for perch are close to (age-groups 2–8) or lower than (age-groups 4–8) observed values. Thus, roach is likely to have enough area for increased abundance in comparison with perch and, under the same environmental conditions, is theoretically capable of producing a more abundant population (which would be an advantage in its competition with perch).

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Relations Between Exploitation, Yield, and Community Structure in Polish Pikeperch (*Stizostedion lucioperca*) Lakes, 1966–71[1]

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BONAR, A. 1977. Relations between exploitation, yield, and community structure in Polish pikeperch (*Stizostedion lucioperca*) lakes, 1966–71. J. Fish. Res. Board Can. 34: 1576–1580.

A review of official fishery records maintained on 43 Polish pikeperch (*Stizostedion lucioperca*) lakes during 1966–71 showed that yield was dependent on exploitation intensity and community structure. Community structure was studied on the basis of three groups of fish: predatory, undesirable, and valuable nonpredatory. The percent of predatory fish was used as an index of community structure. An increase of 1 unit of exploitation intensity increased yield by 0.42–0.50 kg/ha and a 1% increase in predatory fish decreased yield by 0.45–0.49 kg/ha. Undesirable fish predominated in lakes with high yields and predatory fish predominated in lakes with low yields. The largest catches of predatory fish species occurred when their percentage in the total catch reached 25. A more effective regulation of predatory and nonpredatory fish populations may be achieved through controlled exploitation.

Key words: Percidae, European pikeperch, Poland, community dynamics, methodology, predators, exploitation, yield

BONAR, A. 1977. Relations between exploitation, yield, and community structure in Polish pikeperch (*Stizostedion lucioperca*) lakes, 1966–71. J. Fish. Res. Board Can. 34: 1576–1580.

Une revue des statistiques officielles de pêche dans 43 lacs à sandre (*Stizostedion lucioperca*) polonais entre 1966–71 démontre que le rendement dépend de l'intensité de l'exploitation et de la structure de la communauté. Nous avons étudié la structure des communautés en terme de trois groupes de poissons: prédateurs, indésirables et non prédateurs de valeur. Le pourcentage de poissons prédateurs a été utilisé comme indice de structure de la communauté. Une augmentation de 1 unité d'intensité d'exploitation produit une augmentation de rendement de 0.42–0.50 kg/ha, et une augmentation de 1% des poissons prédateurs diminue le rendement de 0.45–0.49 kg/ha. Les poissons indésirables prédominent dans les lacs à hauts rendements, et les poissons prédateurs prédominent dans les lacs à faibles rendements. Les plus grosses prises de poissons prédateurs se font quand leur pourcentage dans la prise totale atteint 25. Une exploitation contrôlée permettrait de régler plus efficacement les populations de poissons prédateurs et non prédateurs.

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THE purpose of this study was to determine the relations between exploitation, yield, and community structure in Polish pikeperch (*Stizostedion lucioperca*) lakes. Relations between intensity of exploitation (jm/ha), an index of the effectiveness of exploitation (kg/jm), percent of predatory fish as an index of community structure and yield (kg/ha) were investigated according to the scheme outlined in Fig. 1.

Pikeperch lakes in Poland are numerous and constitute about 19% of the water surface under fishery management (Leopold and Dabrowski 1974). The surface areas of these lakes are small and in most cases are not larger than 1000 ha. They are shallow (mean depth 1.5–15.0 m) and have low water transparency (0.35–3.00 m) and considerable contents of dissolved solids. They are situated in rich catchment areas, often with intensive agriculture. They are further enriched by numerous effluents from municipal sewage and food processing industries.

The 43 lakes selected for study had surface areas greater than 100 ha and mean pikeperch yields above 1 kg/ha. These lakes comprised about 25% (or about 15,253 ha) of the total surface area of pikeperch lakes in Poland. The data used in this paper were taken from com-

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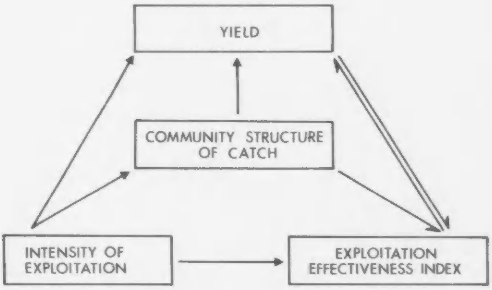
YIELD
COMMUNITY STRUCTURE OF CATCH
INTENSITY OF EXPLOITATION
EXPLOITATION EFFECTIVENESS INDEX

FIG. 1. Scheme of relations between yield, community structure, intensity of exploitation, and exploitation effectiveness index.

mercial catch and exploitation records maintained by state fish farms during the years 1966–71. These records did not include the angling catches, which according to Leopold and Dabrowski (1974) averaged 30% of the total biomass of catches in Polish lakes.

Community structure was studied on the basis of three groups: predatory: eel (*Anguilla anguilla*), pikeperch, northern pike (*Esox lucius*), Eurasian perch (*Perca fluviatilis*) >0.2 kg; undesirable: bream (*Abramis brama*) <0.5 kg, perch <0.2 kg, roach (*Rutilus rutilus*), ruffe (*Gymnocephalus ceruna*), white bream (*Blicca bjoerkna*; and valuable nonpredatory: bream >0.5 kg, tench (*Tinca tinca*), carp (*Cyprinus carpio*).

The terms "valuable" and "undesirable" do not indicate ecological value but rather reflect use in fishing practice and have an economic meaning.

The percentages of the total annual commercial catch from the 43 lakes during 1966–71 (avg. 27.3 kg/ha) represented by the various species and the three groups were:

Species	%
Pikeperch	11.4
Bream >0.5 kg	21.3
Roach	19.0
Bream <0.5 kg + white bream	16.8
Pike	8.8
Eel	7.3
Another undesirable	6.6
Another valuable	5.1
Perch >0.2 kg	2.6
Perch <0.2 kg	1.1
Undesirable species	43.6
Valuable species, nonpredatory	26.4
Predatory species	30.0

Materials and Methods

Both acitve (summer and winter seines with bags) and passive (gill nets, trap nets, entangling nets) gears were used in the fishery. The most intensive fishing (on the average about 80%) occurred during summer and autumn. The active gears (Drabowski et al. 1964; Leopold and Nowak 1964), although much less selective than the passive in regard to the species and size of fish captured, took a greater proportion of the undesirable group. The percent of total yield was generally 1 to 3 times as great with active as with passive gears, regardless of the intensity of exploitation (Fig. 2).

The term "jm" represents a coefficient of relative efficiency of a standard unit of various gears fished. To estimate the fishing or exploitation intensity and the index of effectiveness of exploitation, Leopold (1969) and Leopold and Drabowski (1974) assumed, as stated by the latter authors, the following: "A conventional fishing gear, catching one kg of fish daily, was taken as a standard unit of fishing effort for comparison. Then, based upon long-term catch data from different types of fishing gear and collected in various parts of Poland from hundreds of lakes, the average daily catches of the different types of fishing gear, expressed in kg of fish per day, were calculated. The values thus obtained were considered as standard fishing effort for each fishing gear. Thus, the fishing intensity of a given fishing gear is the product of its standard fishing effort multiplied by the number of days during which it is used. Subsequently, the catch per unit of area, or intensity per unit of area (standard units per ha) can be derived." Leopold and Dabrowski (1974) defined the index of effectiveness of exploitation as "The total fish catch on a given lake divided by the sum of the fishing intensities of all types of fishing gear." This index, used in the simplest manner, provides a relative

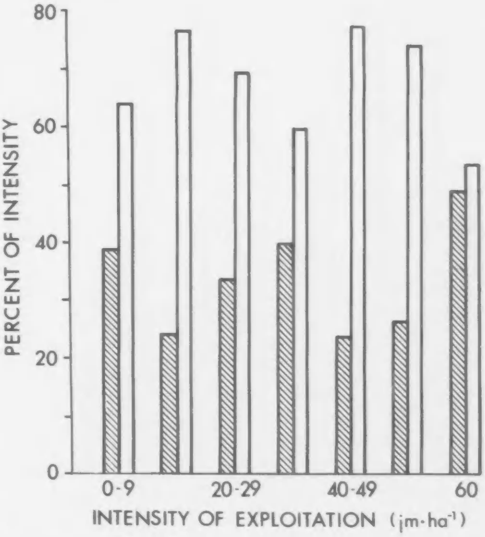

FIG. 2. Structure of the intensity of exploitation in relation to gear type.

measure of the density of a fish stock and also, indirectly, its number.

Regression methods were applied to analyse the data trends. The significance of relations between the variables was estimated using Pearson's correlation coefficient (Guilford 1964). Average values of the exploitation intensities and yields for 1966–71 were used as single statistical observations.

Relations Between Intensity of Exploitation, Effectiveness of Exploitation, and Yield

The relationship between yield and fishing intensity (Table 1, Fig. 3) was highly significant ($r = 0.637$, $P \leqslant 0.01$). An average increase of 1 jm/ha increased the yield by 0.42 kg/ha ($y = 14.56 + 0.42x$, where x = intensity of exploitation in jm/ha and y = yield in kg/ha).

Relations Between Community Structure and Yield

Yield in the lakes investigated was influenced by the community structure. Undesirable fish predominated in lakes with high yields and predatory fish predominated in lakes with low yields (Table 2, Fig. 4). A significant negative correlation existed between yield and percentage of predatory fish ($r = -0.574$, $P \leqslant 0.01$). On the average, a 1% increase in predatory fish produced a decrease in yield of 0.49 kg/ha (Fig. 5).

The catches of particular species groups showed no single tendency with regard to the amount of predatory fish (Fig. 6). Only the catches of undesirable fish declined consistently ($y = 24.72 - 0.43x$). The relationship between the two variables was highly significant ($r = -0.651$, $P \leqslant 0.01$).

The lakes studied can be divided into two groups. The first group, in which predators comprised less than 25% of the total catches, were characterized by high yields (Table 2), an increase in the percentage of predatory and valuable nonpredatory fish and a decline in the percentage of undesirable fish. In the second group were lakes in which the percentage of predatory fish exceeded 25. These lakes had lower yields than the first group (Table 2) and as the percentage of predators increased the percentage of undesirable and valuable nonpredatory fish in the catches decreased.

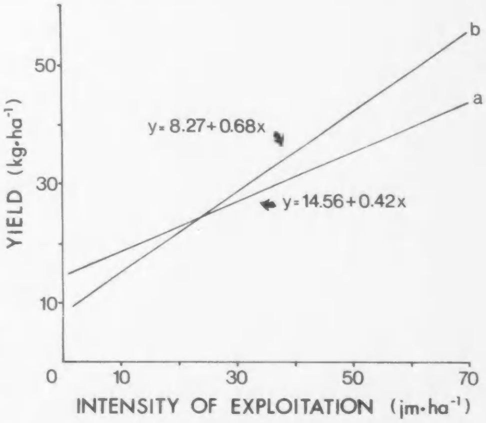

FIG. 3. Relations between yield and intensity of exploitation for (*a*) 43 pikeperch lakes, 1966–71, and (*b*) 224 Polish (Leopold 1969) lakes.

TABLE 1. Relations between intensity of exploitation, average yield of fish, and exploitation effectiveness index for (*a*) 43 pikeperch and (*b*) 224 Polish (Leopold 1969) lakes.

Intensity of exploitation (jm/ha)[a]		Yield (kg/ha)		Exploitation effectiveness index (kg/jm)	
a	*b*	*a*	*b*	*a*	*b*
9.40	6.08	8.70	10.40	0.93	1.71
15.01	14.87	17.94	19.74	1.19	1.33
24.56	24.48	26.39	25.33	1.07	1.03
34.76	34.41	31.20	32.56	0.90	0.95
42.23	44.54	35.57	39.00	0.84	0.88
53.74	54.33	36.40	42.82	0.68	0.79
63.22	65.81	39.50	38.89	0.62	0.59

[a] Averages for values within successive intervals of 10 jm/ha.

Assuming that these observed trends in community structure were due to the influence of predators, then as the predation pressure increased a decrease in catches in the following sequence would be expected: undesirable, valuable nonpredatory, predatory.

A high degree of cannibalism has been observed for perch and pikeperch (Antosiak unpublished data; Połtavczuk 1965; Nagięć 1974; Martyniak unpublished data). In lakes having a small nonpredatory fish component, cannibalism is considerably more frequent than in other water bodies. In lakes with excessive exploitation, which would be disproportionately distributed on predatory and nonpredatory fish, the balance in the numbers of both groups may be disturbed (Bonar 1974).

Multiple Relations of Variables

Exploitation and predation act together to diminish abundance of fish stocks and, indirectly, the total catch. Moreover, the degree of predation depends to a great extent on the intensity and selectivity of exploitation. This indicates the great complexity of the phenomena investigated.

TABLE 2. Average percentages of undesirable and valuable nonpredatory species in the catches in relation to the percentage of predators in 43 pikeperch lakes, 1966–71.

Percent of predators	Yield (kg/ha)	Undesirable	Predatory	Valuable Nonpredatory
0–9.9	26.9	62.5	8.9	28.6
10–19.9	35.6	59.3	15.2	25.6
20–29.9	29.2	36.0	27.0	37.0
30–39.9	23.7	36.3	34.2	29.5
40–49.9	13.7	8.0	48.2	43.8
>50	11.0	7.3	69.1	23.6

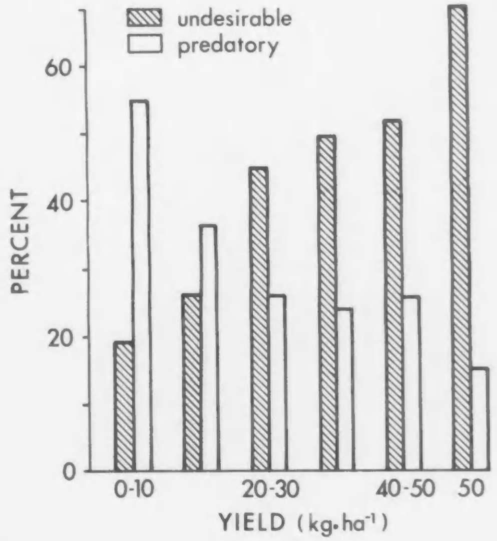

FIG. 4. Percent of predatory and undesirable fish in catches from 43 pikeperch lakes, 1966–71, in relation to yield.

All the factors tested in this paper were interrelated and interacted with each other.

The multiple relationship between yield, exploitation intensity and the percent of predatory fish was statistically significant. These relationships, where x = percent of predators, y = intensity of exploitation (jm/ha), $z_{,}$ = yield (kg/ha) and $z_{,,}$ = index of effectiveness of exploitation (kg/jm), were:

Coefficient of correlation	Multiple regression
0.799	$z_{,} = 25.135 - 0.447x + 0.497y$
0.687	$z_{,,} = 1.941 - 0.017x + 0.015y$

Thus an increase in the exploitation intensity of 1 jm/ha would cause a 0.50 kg/ha increase in yield and a 1% increase in the percentage of predatory fish would cause a 0.45 kg/ha decrease in yield.

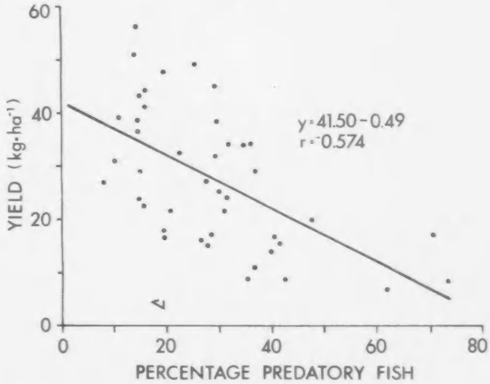

FIG. 5. Relation between average yield of fish and average percent of predators in the catches of 43 pikeperch lakes, 1966–71.

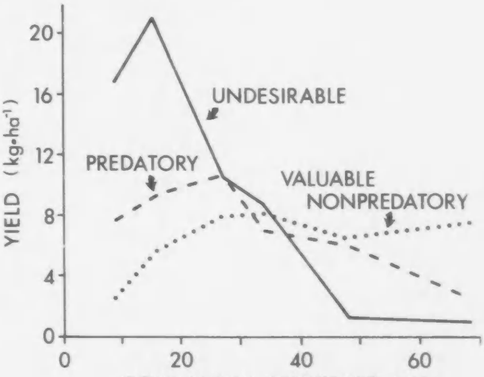

FIG. 6. Relations between average yield of fish and percent undesirable, predatory, and valuable nonpredatory groups as components of community structure.

Both factors also diminish fish stock abundance. The combined pressure of exploitation and predation causes a considerable decrease in the average abundance of fish in pikeperch lakes relative to the Polish lakes studied by Leopold (1969).

This analysis is a simplification of the phenomena investigated. Apart from the variables considered in this study there are a number of other significant factors that decrease stock abundance and the abundance of catches in pikeperch lakes.

General Discussion

It should be expected that continued intensification of exploitation would eventually cause a decrease in yield (Ricker 1958). However, in these 43 pikeperch lakes an increase in exploitation intensity resulted in an increase in yield. This suggests that intensity of exploitation was not sufficient to affect total yield. Leopold (1969), in his investigation of 224 Polish lakes, reached a similar conclusion.

The species compositions of the catches were characterized by a percentage of predatory fish (on the average 30%) which was much higher than the average for most Polish lakes. This may be caused not only by specific biocenotic factors, but also by exploitation, which increased the mortality rates of both predator and prey species. Exploitation may affect species or groups of species of various abundance levels differently and thus consequently disturb the natural mechanisms regulating the numbers of fish.

Exploitation of lakes in Poland was performed mainly with seines, which were more selective on prey species such as roach, bream, white bream and perch than on other species (Dabrowski et al. 1964; Leopold and Nowak 1964). Thus exploitation pressure on the undesirable fish (prey species) was much higher than on the predators.

The second equilibrium factor influencing yield was community structure, expressed as the percentage of predatory fish in the catch. As the percent of predatory fish increased, yield decreased. The largest catches of predator fish species occurred when their percentage of the total catch reached about 25–30. Similar results were presented by Adams and Olver (1977). This suggests that a community structure may exist for which exploitation of predators may be optimized.

Percid production in these 43 pikeperch lakes was less than that suggested from the curve proposed by Colby et al. (1972). It is inferred that the causes for this divergence were species differences between North American and European waters, improper exploitation of fish stocks and the predation pressure exerted on the prey species.

These data explain the influence of predation and community structure on yield and point out that it is possible to interfere in the predator–prey relationship by fishing exploitation. The results may also contribute to a more effective regulation of predatory and nonpredatory fish populations through controlled exploitation.

Acknowledgments

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Pikeperch (*Stizostedion lucioperca*) in its Natural Habitats in Poland[1]

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NAGIĘĆ, M. 1977. Pikeperch (*Stizostedion lucioperca*) in its natural habitats in Poland. J. Fish. Res. Board Can. 34: 1581–1585.

The distribution and biology of pikeperch, *Stizostedion lucioperca*, in Poland are reviewed along with the characteristics of lakes where pikeperch are abundant. The characteristics of these lakes include low mean depth, lack of thermal stratification in summer, and intensive mixing of water. These characteristics are discussed in relation to primary productivity, zooplankton composition, abundance of benthos, and fish harvests in lakes and firths.

Key words: Percidae, pikeperch lakes, harvest, habitat, *Stizostedion lucioperca*

NAGIĘĆ, M. 1977. Pikeperch (*Stizostedion lucioperca*) in its natural habitats in Poland. J. Fish. Res. Board Can. 34: 1581–1585.

Nous passons en revue la distribution et la biologie du sandre, *Stizostedion lucioperca*, en Pologne, ainsi que les caractéristiques des lacs où l'espèce est abondante. Parmi les caractéristiques de ces lacs, on note une faible profondeur moyenne, un manque de stratification thermique en été et un mélange intensif de l'eau. Nous examinons ces caractéristiques en relation avec la productivité primaire, la composition du zooplancton, l'abondance du benthos et la récolte de poissons dans les lacs et les bras de mer.

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THIS paper is a brief review of the distribution and biology of pikeperch (*Stizostedion lucioperca*) in Poland, particularly in relation to environmental characteristics of lakes and firths.

Available information indicates that Poland is close to the western limit of natural distribution of the pikeperch. For example numerous bones of pikeperch dating from the 10th to 13th centuries have been found in archeological excavations from various rivers and lakes in Poland (Susłowska 1967; Dąbrowska 1967). Occurrence of pikeperch in areas west of the River Elbe resulted from introductions after the 16th century (Steffens 1960). This species was first stocked in the River Main in 1883 (Schmidt 1970), and identified in Holland in 1888 (Willemsen 1977), and in France after World War I (Goubier 1975).

The most abundant stocks of pikeperch in Poland are found in the lower courses of rivers and Baltic bays such as Vistula Firth (area 815 km^2) and the Firth of Szczecin (area 800 km^2). The total area of lakes in Poland is approximately 2700 km^2, and of this 510 km^2 has been characterized as pikeperch in type.

Total annual landings of pikeperch from commercial fisheries during 1948–75 was 400–1000 m t (Fig. 1). The distribution of lakes and firths with major pikeperch fisheries is shown in Fig. 2.

Characteristics of Pikeperch Lakes

Polish lakes in which pikeperch are abundant are characterized by low mean depths, lack of thermal stratification in summer, and intensive mixing of water. They are eutrophic, produce

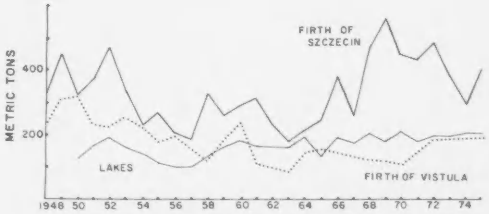

FIG. 1. Annual catches of pikeperch in lakes and two firths of Poland, 1948–75 (from unpublished data of Marine Fishery Institute, Gdynia and Inland Fisheries Institute, Olsztyn).

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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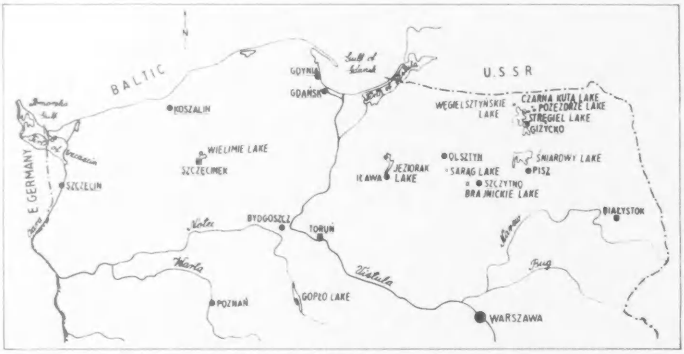
N
BALTIC
Gulf of Gdansk
U.S.S.R
GDYNIA
GDAŃSK
KOSZALIN
WIELIMIE LAKE
SZCZECINEK
E. GERMANY
SZCZECIN
WĘGIELSZTYŃSKIE LAKE
CZARNA KUTA LAKE
POZEZDRZE LAKE
STRĘGIEL LAKE
GIZYCKO
OLSZTYN
ŚNIARDWY LAKE
JEZIORAK LAKE
IŁAWA
SARĄG LAKE
PISZ
SZCZYTNO
BRAJNICKIE LAKE
BIAŁYSTOK
BYDGOSZCZ
TORUŃ
Noteć
Warta
Vistula
Bug
POZNAŃ
GOPŁO LAKE
WARSZAWA

FIG. 2. Distribution in Poland of lakes and firths with major pikeperch fisheries.

frequent algal blooms, and have low Secchi disc transparencies (often less than 0.5 m).

Mikulski (1964) studied selected pikeperch lakes and related pikeperch catches to the following lake characteristics: area, mean depth, total content of organic substances (measured as biological oxygen demand — BOD), alkalinity, and pH. He found yields were greatest in lakes with highest organic content (Fig. 3) and in shallow lakes. No correlations were found between levels of pikeperch catches and lake area, alkalinity, or pH.

Lack of thermal stratification in summer appears to be an important characteristic of pikeperch lakes. Patalas (1960b) distinguished five types of thermal stratification (grades of stability): from type I, shallow and well mixed, with high potential for resuspension of sediments through to type V, with shallow epilimnion, high thermal gradient in the metalimnion and deep and cold hypolimnion (Fig. 4). All pikeperch lakes represent well-mixed types I and II (Table 1, Giziński 1974).

High primary productivity appears to be associated with pikeperch lakes. Patalas (1960b) developed a productivity index based on ranking factors related to geomorphology of drainage, water renewal, and morphology of the lake basin. Index values range from 1 for extremely unproductive lakes to 6 for highly productive lakes. All pikeperch lakes were characterized by very high productivity with an index ranging from 3.8 to 5.3 (Table 1).

Zooplankton in pikeperch lakes is composed of rather ubiquitous species. The most common forms in the summer plankton are *Mesocyclops* sp., *Daphnia cucullata*, and *Chydorus sphaericus* (Bittel 1964).

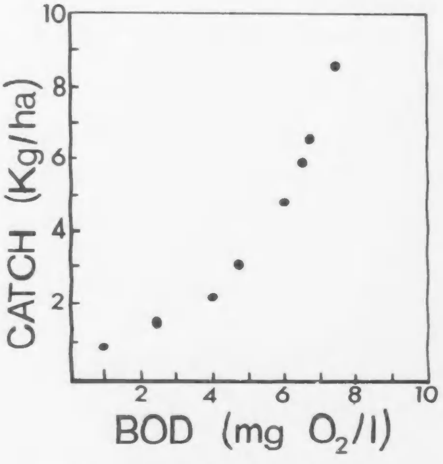

FIG. 3. Pikeperch catches and BOD of water in eight Polish lakes (from Mikulski 1964).

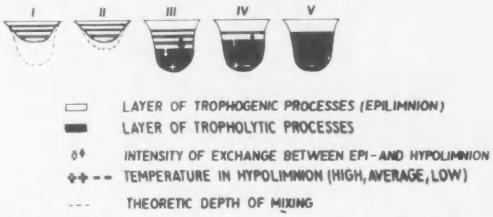
I
II
III
IV
V
LAYER OF TROPHOGENIC PROCESSES (EPILIMNION)
LAYER OF TROPHOLYTIC PROCESSES
INTENSITY OF EXCHANGE BETWEEN EPI- AND HYPOLIMNION
TEMPERATURE IN HYPOLIMNION (HIGH, AVERAGE, LOW)
THEORETIC DEPTH OF MIXING

FIG. 4. Grades of stability of lakes (from Patalas 1960a).

There is no real profundal zone in well-mixed pikeperch lakes. Due to low transparency the bottom of the limnetic zone is free of rooted vegetation. Sediments vary from lake to lake, but black gyttja and red sediments of jelly-like structure are frequently found and are associated with low faunal biomass and low species diversity (Mikulski 1964). Pieczyńska et al. (1963) found the mean value of bottom fauna biomass in 42 lakes to be 6.7 g/m² (0.2–37.0 g/m²), whereas the mean biomass in four pikeperch lakes was

TABLE 1. Some ecological features of seven pikeperch lakes in Poland (after Patalas 1960a, b; Pieczyńska et al. 1963; Giziński 1974). See text for explanation of stability grades and primary productivity.

	Czarna Kuta	Wegielsztyn	Pozezdrze	Stregiel	Wielimie	Gopło	Jeziorak
Type	pond	pond	pond	Eutrophic lakes			
Area (ha)	25.2	77.8	124.3	411.0	1865	2180	3219
Depth, maximum (m)	3.8	2.0	4.0	14.0	5.5	16.6	12.0
Depth, mean (m)	1.4	1.3	2.2	3.6	2.2	3.6	4.1
Maximum effective length of axis (km)	1.15	1.10	2.20	3.85	7.00	7.20	7.25
Maximum effective width of axis (km)	0.45	1.10	0.80	1.95	4.90	2.50	3.73
Average effective length of axis (km) (D)[a]	0.80	1.10	1.50	2.90	5.95	4.85	5.49
Theoretical mixing depth (m) ($4.4\ D^{\frac{1}{2}}$)	3.9	4.6	5.4	7.5	10.7	9.7	10.3
Ratio of theoretical mixing depth to average depth (4.4 D/avg. depth)	2.79	3.54	2.45	2.08	4.86	2.69	2.51
Grade of stability	II	I	I	II	I	I	I
Primary productivity	4.2	5.1	5.3	4.6	5.3	4.3	3.8
Bottom fauna							
No./m^2					847	646	538
mean biomass (g/m^2)	0.2	0.7	5.6	4.8			
Average yield (kg/ha) (1950–75 unless indicated otherwise)							
pikeperch	8.3[d]	1.9[c]	1.0	2.9	4.8[f]	2.5[b]	5.3[b]
bream	10.3	8.4	13.4	11.5	37.4[e]	9.9[b]	7.9[b]
eel	0.9	1.7	8.0	2.9	4.1[e]	3.5[b]	1.4[b]

[a]Arithmetical mean for maximum effective length and maximum effective width; [b]1952–75; [c]1953–75; [d]1957–75; [e]1964–75; [f]1966–75.

much lower — 2.8 g/m^2 (0.2–5.6 g/m^2). Similarly, Giziński (1974), in studying 23 lakes, found an overall mean of 1850 organisms/m^2 whereas those classified as pikeperch lakes had a mean of 667 organisms/m^2. The most common invertebrates found by Pieczyńska et al. (1963) and Giziński (1974) were chironomid larvae, (usually *Chironomus plumosus*), *Chaoborus* larvae, and oligochaetes. The lack of abundant bottom fauna in pikeperch lakes may be caused by the presence of at least three species of bottom feeders: bream (*Abramis brama*), eel (*Anquilla anquilla*), and ruffe (*Gymnocephalus cernua*). However, opinions vary regarding the way in which fishes affect the biomass of bottom fauna and most authors consider that this effect is insignificant (Kajak 1968). The above data suggest that, although abundance and composition of bottom fauna may indicate lake type, they do not affect production of pikeperch directly.

The main producers of pikeperch in Poland are the Firths of Vistula and Szczecin which yield high pikeperch catches per unit area. Mean catches during 1948–75 were 5.4 kg/ha for the Firth of Vistula and 6.5 kg/ha for the Firth of Szczecin (Marine Fishery Institute, Gdynia, unpublished data). Both firths have many features in common with pikeperch lakes (Stangenberg 1958). They are shallow (mean depth of the Vistula Firth is 2.6 m, that of Szczecin 3.4 m) and have low transparencies (Secchi disc frequently 16–18 cm), intensive mixing in the whole water column, and high content of organic substances. The lakes and firths differ only in salinity which ranges from 1.5 to 4.0‰ in the Firth of Vistula, and from 0.5 to 2.0‰ in the Firth of Szczecin (Rózańska 1967). Predominant zooplankters are rotifers, larvae of the mollusc *Dreissena polymorpha*, and the brackish mysid *Neomysis vulgaris*. *Eurytemora* and *Acartia* spp. represent Copepoda in the Vistula Firth, which has the higher salinity (Rózańska 1967). Szczecin Firth has more freshwater *Cyclops* and *Diaptomus* spp. as well as *Cladocera* spp. Both firths are very rich in plankton (Swiezawska–Wiktor 1957). In addition, bottom fauna is more abundant in firths than in pikeperch lakes (Table 2).

Some Biological Characteristics of Pikeperch Populations

Spawning takes place in May in both lakes

TABLE 2. Number and biomass of total benthos and biomass of Mollusca in four Polish waterbodies.

	No./m^2 Total benthos	Biomass (g/m^2) Total benthos	Biomass (g/m^2) Mollusca	Author
Gopło Lake	646			Giziński (1974)
Jeziorak Lake	538			”
Vistula Firth	1973–6013^a	9.3–33	0.0–0.03	Zmudziński (1957)
Szczecin Firth	597–27192^a	2.6–1245	0.41–1198	Wiktor & Wiktor (1954)

^{a}Number and biomass depend on character of bottom.

and firths. Tesch (1959) suggested that ovulation is directly stimulated by changes in atmospheric pressure. A water temperature of 12°C (Deelder and Willemsen 1964; Muntian and Reznitchenko 1967) is considered the thermal threshold for the onset of spawning. The age of spawning fish ranges from 2 to 10 yr in firths and from 3 to 8 yr in lakes. Terlecki (1976) found that the relationships between absolute fecundity (F_a), length (L) and weight (W) for 262 pikeperch females from Lake Jeziorak were represented by:

$$\log F_a = 0.25997 + 3.1141 \log L$$
$$\log F_a = 2.28899 + 1.0227 \log W$$

In five Polish waterbodies the highest fecundity was recorded (Terlecki 1976) for Lake Wielimie in Western Poland, perhaps due to longer growing season and higher water temperatures.

Growth rate and food composition were examined for pikeperch fry in the Firth of Szczecin (Wiktor 1964) and Jeziorak Lake (Nagięć 1966; Murawska 1976). Initially, young (age 2–3 wk) fry feed on small zooplankton (Rotatoria, Copepoda and Cladocera, and larvae of *Dreissena polymorpha*). At age 4–6 wk the fry often change food, *Neomysis vulgaris* and tachyplanktonic larvae of *Chaoborus flavicans* becoming the preferred food. In waters where plankton is limited, pikeperch exhibit cannibalism and also feed on fry of smelt (*Osmerus eperlanus*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*). This change in diet from plankton to fishes is accompanied by a shift from an unimodal to a bimodal length-frequency distribution with the largest individuals feeding exclusively on fishes.

Various authors (Martyniak 1975; Fopp 1971; Szypuła 1964; Horoszewicz 1964; Filuk 1962) have studied the diets of adult pikeperch. The diet of pikeperch in a single waterbody was found to change from year to year and to be different for different waterbodies, but in general, smelt and spawning herring (*Clupea harengus harengus*) were the main food items in firths. In lakes where smelt do not occur, roach and perch are the main fishes in the diet. When pikeperch reach a body length of 40 cm, the consumption of bream, white bream (*Blicca bjoerkna*) and ruffe increases. Cannibalism on young-of-the-year pikeperch seldom occurs in Lake Jeziorak.

Growth rate of young pikeperch is fastest in lakes (e.g. Lake Jeziorak) where fry are forced to be piscivorous rather early. In lakes rich in zooplankton (e.g. Lake Czarna Kuta), feeding of fish is delayed, growth is slower and size of fry at the end of the first growing season is smaller. It is possible that the faster growth rate in Lake Jeziorak is attained at the cost of the number and biomass of a given generation, and that with slower but more even growth in Lake Czarna Kuta and the firths, relative biomass of a given generation is higher. This supposition is supported by the commercial catch data which indicate higher catches per unit area in the firths and Lake Czarna Kuta despite exceptionally high fishing intensity in Lake Jeziorak.

Mortality rates of pike perch in Poland range from 58% in less intensively exploited populations to 90% in populations subject to intensive exploitation (Nagięć 1964; Wiktor 1962).

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Environmental Conditions of Percid Waters in Central Europe[1]

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ENTZ, B. 1977. Environmental conditions of percid waters in central Europe. J. Fish. Res. Board Can. 34: 1586–1591.

A brief review of the limnology of central European waters indicated that, except for calcium in the bottom sediments, mesotrophic lakes were intermediate in nutrient concentrations between oligotrophic and eutrophic waters. Other biotic characteristics also attained maxima in mesotrophic lakes. For example, the existence of distinctive phytoplankton, invertebrate, and fish communities, implied certain qualitative properties of mesotrophic waters rather than only quantitative intermediacy on the oligotrophic–eutrophic cline. These properties, in part, represent some aspects of percid habitat that differ from those of other fish communities.

Key words: Percidae, algae, bottom sediments, cultural effects, eutrophication, limnology, mesotrophy, trophic levels, primary production

ENTZ, B. 1977. Environmental conditions of percid waters in central Europe. J. Fish. Res. Board Can. 34: 1586–1591.

Une brève revue de la limnologie des eaux de l'Europe centrale indique que, sauf pour le calcium dans les sédiments du fond, les lacs mésotrophes sont intermédiaires entre les eaux oligotrophes et eutrophes quant aux concentrations d'éléments nutritifs. D'autres caractères biotiques atteignent également un maximum dans les lacs mésotrophes. Par exemple, l'existence de communautés distinctives de phytoplancton, d'invertébrés et de poissons laisse supposer certains propriétés qualitatives des eaux mésotrophes plutôt que seule une condition intermédiaire quantitative sur un gradient oligotrophe–eutrophe. Ces propriétés représentent en partie certains aspects de l'habitat des percidés qui diffèrent de celles d'autres communautés de poissons.

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IN this review I define the range of environmental conditions of central European lakes in which percids thrive, with emphasis on both abiotic and biotic properties of mesotrophic waters. I then compare these with the same environmental parameters of oligotrophic and eutrophic waters. Lake Balaton is singled out as formerly a prime percid environment which has evolved to less than optimum through cultural influences.

Europe, especially its central part, belongs to one of the Northern Hemisphere's physiographically most differentiated territories (Valdász 1960; Bulla 1962). In addition to high, snow-covered mountain ranges it has many hilly areas with a dense web of river and creek valleys as well as extended flat countryside with moderately cold winters and warm but not exceptionally hot summers.

Late in the Kainozoic Epoch there were three major areas in central Europe differing in physiographic development. These differences had profound effects on the morphology of their corresponding watersheds, namely: the Alps in the west, the Baltic region in the north, and areas in the southeast affected by Pontic influences (Vadász 1960).

The Alps and the Carpathian Mountains developed simultaneously during the Miocene periód, forming three important river systems: the Rhine, the Rhone, and the Danube. Of the Rhine and the Rhone watersheds, only the upper reaches belong to central Europe, but almost all the Danube watershed is included therein. The faunal elements of these river systems are closely similar due to their interconnection during the late glacial period (Thienemann 1950).

The area between the Alps, the Carpathian Mountains, and the Baltic Sea, the German–Polish Lowland, or Sarmatian Lowland, includes many rivers and lakes of glacial origin.

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The middle and the lower part of the Danube watershed, with their hilly or flat areas within the Carpathian Basin and the neighboring eastern lowlands, belong to the Pannonic–Pontic territories. These areas were without permanent ice-cover during the last glacial period but were affected several times by inundation and recession of the shallow Pannonic–Pontic seas.

This region contains one of the world's largest dolomite accumulations and is generally very rich in marine or freshwater sedimentary rocks such as dolomites and limestones bearing highly buffered waters of relatively high carbonate-hardness. According to Collette and Bănărescu (1977), the Danube watershed was the radiation site whence the percids dispersed throughout most of Europe and a large part of Asia and North America.

Regional Distributions of Fish–Fauna

The central European waters, consequently, are divided into three major regions (Busnița 1967): the upper, or salmonine–coregonine, region; the middle, or barbel (*Barbus*)–grayling (*Thymallus*) region; and the lower region, dominated by cyprinids (e.g. carp and bream).

This segregation of fish–fauna is apparent in both altitudinal and horizontal (i.e. east–west) directions. Altitudinally, the rivers with sources in the high mountains show these changes along their courses. As an example, in its upper regions, the Danube River receives tributaries which flow mostly from the Alps and which are inhabited by trout and coregonine species, as in waters in Switzerland, Austria, and Germany. These rivers have fast currents, their waters are permanently cool and transparent or, if turbid, show inorganic turbidity as primary production is low. There is little organic sedimentation and the substrate is usually composed of boulders, stones or coarse gravel.

In the barbel-grayling region, the currents are slower than in the upper salmonine-coregonine region, the water is usually more turbid and in some sections sandy sediments are formed. The temperature is somewhat higher without a corresponding decrease in oxygen saturation. The fauna are notably distinct from those in the upper region. Salmonines and coregonines are gradually replaced by the characteristic *Barbus* genus (Cyprindae), a few other cyprinids, the northern pike (*Esox lucius*) and several percids (e.g. *Perca fluviatilis*, *Stizostedion lucioperca*, and *Gymnocephalus cernua*).

In the lower region, the rivers have warmer, sluggish waters of a brownish or greenish turbidity. Here most of the common fishes are cyprinids (*Abramis* spp., *Cyprinus carpio*, *Carrassius vulgaris*), silurids, and acipenserids. Primary production may reach high values, particularly in lakes and in the sluggish side-arms of the rivers, where the oxygen saturation may become low, especially at night in summer. The substrate is soft, usually muddy or covered by clay. The sediments may attain remarkable depths, particularly on the Hungarian Great Plain and in Yugoslavia, Rumania, and Bulgaria.

Typology of the Waters

The widespread water bodies vary widely concerning age and morphology as well as ecological properties. There are both natural waters and reservoirs with juvenescent characteristics and very slight sedimentation in contrast with senescent basins containing thick layers of sandy or muddy sediments, along with many intermediate types.

Following the fundamental work of Forel in Switzerland in 1892, several scientists among the many classifications, such as Naumann (1921) in Sweden and Halbfass (1923) and Thienemann (1926) in Germany proposed a system of lake typology based on biotic and abiotic features. The most common ones were based on nutrient characteristics, as in the oligotrophic–eutrophic series.

It is generally considered that oligotrophic waters are of juvenescent character, being transparent and having low nutrient content and virtually no sediments. They may be altered in time by natural eutrophication into senescent, turbid, eutrophic waters with high nutrient content and deep sediment layers on the substrate. This process is usually slow in the absence of cultural influences and may be measured in thousands or tens of thousands of years.

Between the initial and final stages of the eutrophication process, there are transitional, mesotrophic conditions. During the transition, the abiotic factors as well as the fauna and the flora undergo basic changes. The beginning and the final stages may be characterized more definitively than the intermediate stage of the transitional process.

There are several species or families characteristic of oligotrophic conditions, such as salmonines and coregonines. Others, such as most cyprinids and silurids, are inhabitants of highly eutrophic waters. Percids are found predominantly in mesotrophic waters or in slightly eutrophic water basins, both types being widely distributed in central Europe.

Characterization of Trophic Types

As stated by Elster (1958), a rigorous description of waters defining the trophic types as mutually exclusive is unlikely. An alternative is to consider different physical, chemical (Table 1)

TABLE 1. Some chemical properties of central European lakes on the basis of the oligotrophic–eutrophic series

Characteristic	Oligotrophy	Mesotrophy	Eutrophy
O_2 (vertical distribution)	Orthograde	Slightly clinograde	Strongly clinograde
O_2 required for respiration and oxidation ($cm^3 \cdot mo^{-1}$)	0.76	0.76–1.64	1.64
O_2 consumption by sediments	Low	Moderate	High
Organic content of sediment (% of dry weight)	11–20	17–30	18–61
Ca content of sediment	Low	Relatively high	Relatively low

TABLE 2. Algal species inhabiting lakes of the oligotrophic–eutrophic series in central Europe (after Rawson 1956).

Oligotrophic species	Mesotrophic species	Eutrophic species
Asterionella formosa	*Fragilaria crotonensis*	Predominant:
Melosira islandica	*Ceratium hirundinella*	*Microcystis flos-aquae*
Tabellaria fenestrata	*Pediastrum boryanum*	
Tabellaria flocculosa	*Pediastrum duplex*	
Dinobryon divergens	*Coelospherium naegelianum*	
Fragilaria capucina	*Anabaena* spp.	
Staurastrum sp.	*Aphanizomenon flos-aquae*	
Melosira granulata	*Microcystis aeruginosa*	

and biological aspects to provide a more comprehensive picture of natural waters as they vary at the different trophic levels.

Chemical properties — Some chemical properties as shown in Table 1 are most characteristic towards the end of the summer stagnation period. In oligotrophic lakes dissolved oxygen concentrations are similar between surface and bottom whereas in eutrophic lakes the bottom waters usually show an oxygen deficit at this time of year. Mesotrophic lakes occupy an intermediate position in this regard.

A hypolimnetic oxygen deficit (Hutchinson 1957; Dussart 1966), concerning quantities of oxygen required for respiration and oxidation, and oxygen consumption by the sediments follow a similar cline from oligotrophic (low) to eutrophic (high) conditions (Table 1).

Calcium contents in lake sediments, however, reach their highest values in mesotrophic lakes (Rybak 1965; Table 1). This suggests a truly qualitative difference between mesotrophic waters and those of oligotrophic or eutrophic characteristics, and that mesotrophy is not quantitatively intermediate between oligotrophy and eutrophy in all instances.

Biological aspects — There are numerous "indicator" organisms (Rawson 1956) distinctive of the three trophic types of water. Various algae of these kinds have been listed according to their trophic requirements (Table 2). It may be seen from Table 2 that distinctive qualitative differences exist in the algal flora, not only between oligotrophic and eutrophic lakes but also between mesotrophic waters and the other two trophic types. These qualitative differences tend to emphasize mesotrophy as distinctly different from oligotrophy and eutrophy when measured by certain qualitative characteristics.

Nygaard and others have shown that the trophic type of water body may be indicated by the proportions of members of certain algal groups. On the basis of these findings, several formulas have been developed. One of the most suitable is that of

$$\text{Nygaard (1947): } C = \frac{Cy + Ch + Ce + Eu}{De}$$

The sum of the Cyanophyta + Chloroccales + Euglenina + Centrales species is divided by the number of Desmidiaceae species. If the quotient (C) is less than 1, the water is oligotrophic. If it ranges between 1 and 2.5, the water body is mesotrophic and if it is more than 2.5, the water is eutrophic.

Similarly, trophic conditions may be characterized by the number of algal cells or the chlorophyll *a* content within a certain volume of water (Table 3). Primary production expressed in organic carbon is likewise suitable to characterize the trophic conditions.

Among the different animal groups there are

TABLE 3. Numbers of algal cells, chlorophyll *a* contents, and daily values of primary production in central European waters of the oligotrophic–eutrophic series. Adapted from Felföldy (1974) and Hübel (1971).

	Oligotrophic	Mesotrophic	Eutrophic
Number of algal cells ($10^6 \cdot \ell^{-1}$)	0.05	0.1–0.5	1.0
Chlorophyll *a* content ($mg \cdot m^{-3}$)	3.0	10–20	50
Primary production ($mgC \cdot m^{-2} \cdot day^{-1}$)	100–300	300–700	700–2000

certain species which are particularly unique forms for certain trophic types. As is well known, Thienemann (1922) based his theory of lake typology on the presence or absence of certain chironomid larvae. Some typical stenoxybiont chironomids such as *Tanytarsus lugens* and *Heterotrissocladius subpilosus* are found in oligotrophic lakes, and some forms such as *Microtendipes chloris*, *Glyptotendipes gribekoveni*, *Polypedilum nebeculosum*, *Sergentia coracina*, *Procladius shuse*, and *Pelopia punctipennis* (Kajak and Dusoge 1975) are characteristic of eutrophic lakes. Euryoxybiont forms such as *Chironomus plumosus* are most representative of eutrophic lakes.

Morphoedaphic Index — Ryder's (1965) morphoedaphic index (MEI) has been useful for the classification of trophic conditions (Ryder 1972). This index is now used in its metric form

$$(\text{MEI} = \frac{\text{Total dissolved solids } (\text{mg}/\ell)}{\text{Mean depth (m)}}.$$

For the central European lakes, those that are mesotrophic have been defined as having an MEI range of between 18.0 and 21.9, and oligotrophic and eutrophic lakes as having values of <18 and >22 or higher, respectively. These values depart considerably from those of Ryder et al. (1974), but the latter authors were dealing with a much narrower range of north-temperate lakes and, as mesotrophy (based on nutrient values) tends to be a relative designation, no apparent contradiction exists.

Temperature Conditions

The previous description of the various biotic and abiotic properties of the mesotrophic lakes has been understood to constitute a general preferendum of conditions for percids. Temperatures, however, may best be described according to their limiting effects on the percid communities.

Temperature preference for spawning by the common European percids ranges between 10 and 14°C, and maximal growth is attained between 22 and 28°C (Willemsen 1977). Temperatures above 30°C may be unsuitable or even lethal for them (Weatherley 1963). Consequently, percids are absent from the permanently cold waters of the high mountains, but are widespread in hilly or lowland areas all over central Europe.

Cultural Influences and Fish Stocks

Lake Balaton, once a prime environment for the growth and reproduction of percid species, has through the intervention of human activities declined in recent years. For example, in fish stocks of areas where a fishery is not conducted, the predatory species because of their piscivorous feeding habits and larger mean size are of great importance in maintaining appropriate steady-state ratios between predator and the more abundant prey species. If in such areas an intensive fishery is developed, the contribution of predatory fish can reach 30–50% of the total yield as calculated by weight (Chevalier 1977). Percids, as primarily predatory fishes, play an important role, therefore, in temperate waters of central Europe. Intensive fisheries have in time — as is well known — an unfavourable selective effect on stocks of predatory fishes, including percids. As an example, the yield trends of two *Stizostedion* species may be compared in two mesotrophic lakes (Table 4), Balaton, and Rainy Lake in south-central Canada.

It may be seen that over the years the percid component of the yield declined markedly. This phenomenon was probably caused additionally by the regulation of lake levels resulting in adverse environmental stresses during and after spawning. In Lake Balaton, several steps have been undertaken to increase the pikeperch stocks but there is still a slow but definite decrease in their contribution to total yield.

Cultural eutrophication — Although the fishing effort in Lake Balaton remained constant from

TABLE 4. Percentages of economically valuable percids in the total fish yields of a central European and a North American lake. These lakes were selected for comparison because of relative similarities in fish stocks, area, and latitude.

Years	*Stizostedion lucioperca* Lake Balaton, central Europe	Years	*Stizostedion vitreum vitreum* Rainy Lake, North America[b]
up to 1845[a]	15–20 (estimate)	up to 1947	30
1900–30[a]	18.1		
1930–60[c]	8.7	1948–63	20
1961–73[d]	8.1	1964–74	10
1974–75[e]	5.4		

[a] Lukács (1932); Illésy (1931).
[b] Chevalier (1977).
[c] Ribiánszky and Woynárovich (1962).
[d] Biró (1977).
[e] Hungarian Academy of Sciences, Biological Research Institute.

1957 to 1975, a continual decrease in the percentage of the preferred Hungarian fish, the "fogas," *Stizostedion lucioperca*, occurred although the lake was known as a famous percid lake. Similarly, the numbers of other percids such as *Stizostedion volgense* and the ruff (*Gymnocephalus cernua*) decreased; others disappeared, like the Eurasian perch (*Perca fluviatilis*). These phenomena may be explained by the cultural eutrophication processes, which can be especially effective in mesotrophic lakes.

The cultural eutrophication of Lake Balaton started in the 1940s, but has been accelerated markedly in the last decade in association with the massive applications of chemical fertilizers and the massive sewage disposal originating from household and animal husbandry.

Studies using the ^{14}C techniques concerning the primary production of the lake by Herodek and Tamas (1975, 1976) revealed that between 1960 and 1975 the rate of primary production increased about 15-fold in the southwest areas of the lake, which were particularly affected by tributaries. These sections of the lake have already reached the hypertrophic stage. Concomitantly, the rate of eutrophication was not nearly as rapid in the northeast areas, where there are no major tributaries. In this area, in 1972, primary production was 50% higher than in 1961. In 1976 the corresponding values were five times those of 1961 (Herodek and Tamas 1976).

Eutrophication may be favorable to a certain extent for some fish stocks, but effects are not equally applicable to all fish families. Above a certain trophic level conditions become less favorable for percids, but are still increasingly favorable for cyprinids. Consequently, the slow, decreasing trend of the pikeperch stocks in Lake Balaton may have been induced by cultural processes in recent years.

Toxic effects — Fertilizers, pesticides, and their metabolites, after being washed into natural waters, accumulate in freshwater organisms, sometimes causing detrimental effects. These effects were unequal on ecologically different fish groups. Gradually accumulated pesticides may reach peak values within the highest trophic level, the level of predatory fishes (Lindeman 1942). It is therefore almost self-evident that during a catastrophic mortality in Lake Balaton in 1965, before the acceleration of eutrophication, fishkill due to pesticides killed about 40% of the pikeperch population. During that year a decline of more than 50% was observed in the yield. The losses were compensated for about 4 yr after the stress was imposed. On the other hand, the less valuable fish species appeared to be less affected although many of them perished during the same fishkill.

The total annual catches from 1965 to 1975 in Lake Balaton remained almost unaffected in quantity but were by far less valuable because of their altered species composition.

Conclusion

That mesotrophic waters serve best to provide the percid community with all of its life necessities is implicit in the observation that where percids form the largest standing crops, constitute significantly large proportions of the total yield, and are diverse in both form and function — therein we have optimum environmental conditions for growth, production and reproduction of the various percid species and consequently high survival rates.

Whereas mesotrophic waters on the basis of nutrients fit on a line between oligotrophic and eutrophic waters, certain characteristics point to the existence of optima in mesotrophic lakes suggesting a real qualitative difference between mesotrophy on the one hand and eutrophy and oligotrophy on the other. Some of those optima are calcium content in the sediments as well as the existence of distinct mesotrophic communities of phytoplankton, invertebrates, and fishes. These optima point to the existence of qualitatively different abiotic and biotic conditions in mesotrophic lakes rather than the expected quantitative intermediacy on the oligotrophic–eutrophic cline. Consequently, our observations are consistent and support the observed structure and transformation of percid communities as proposed by Ryder in Kerr (1977).

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Limnological Characteristics of Ontario Lakes in Relation to Associations of Walleye (*Stizostedion vitreum vitreum*), Northern Pike (*Esox lucius*), Lake Trout (*Salvelinus namaycush*), and Smallmouth Bass (*Micropterus dolomieui*)[1]

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Commonest lake types of the 15 combinations of four fish species (walleye, *Stizostedion vitreum vitreum*; northern pike, *Esox lucius*; lake trout, *Salvelinus namaycush* and smallmouth bass, *Micropterus dolomieui*) were walleye–pike (22%), pike "only" (19%), lake trout "only" (16%) and smallmouth bass "only" (10%). Lake trout–walleye and lake trout–walleye–smallmouth bass types were extremely rare. Lake depth and area were variables of greatest significance in distinguishing lake types by discriminant analysis. Climatic factors explained the general geographic distribution of smallmouth bass. Hypotheses to explain the low frequency of walleye in small lakes include possibilities of (1) low probability of successful coexistence of pike and walleye, (2) lack of wind fetch to clear spawning areas, and (3) "Lebensraum requirement" of the walleye.

Key words: limnology, Percidae, methodology, Ontario lake types, *Stizostedion vitreum vitreum*, *Esox lucius*, *Salvelinus namaycush*, *Micropterus dolomieui*, distribution, associations

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Les types de lacs les plus communs quant aux 15 combinaisons de quatre espèces de poissons (doré jaune, *Stizostedion vitreum vitreum*; grand brochet, *Esox lucius*; touladi, *Salvelinus namaycush*; et achigan à petite bouche, *Micropterus dolomieui*) sont les suivants: doré jaune–grand brochet (22%), grand brochet « seulement » (19%), touladi « seulement » (16%) et achigan à petite bouche « seulement » (10%). Les types touladi–doré jaune et touladi–doré jaune–achigan à petite bouche sont extrêmement rares. La profondeur et la superficie du lac sont les variables les plus importantes lorsqu'on sépare les types de lacs par analyse discriminante. La distribution géographique générale de l'achigan à petite bouche s'explique par des facteurs climatiques. Parmi les hypothèses pouvant expliquer la basse fréquence du doré jaune dans les

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petits lacs, on compte (1) le peu de probabilité d'une coexistence réussie du grand brochet et du doré jaune, (2) l'absence de zone génératrice de vent pour nettoyer les frayères, et (3) le « Lebensraum » dont le doré jaune a besoin.

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In this paper, attempts are made to develop an objective classification, by means of limnological characteristics, of the 15 possible associations of four important game fish species in Ontario lakes (walleye, *Stizostedion vitreum vitreum*; northern pike, *Esox lucius*; lake trout, *Salvelinus namaycush*; and smallmouth bass, *Micropterus dolomieui*). Analysis is based on data in the lake survey files of the Fisheries Branch of the Ontario Ministry of Natural Resources. The lakes were surveyed between the early 1960s and 1974 but principally after 1968; survey methods were described by Martin and Olver (1976). After some preliminary screening of records, about 2500 lakes were selected for discriminant analysis, located between 42 and 52°N and representing all districts except Moosonee of the 49 administrative districts (Fig. 1) of the Ontario Ministry of Natural Resources.

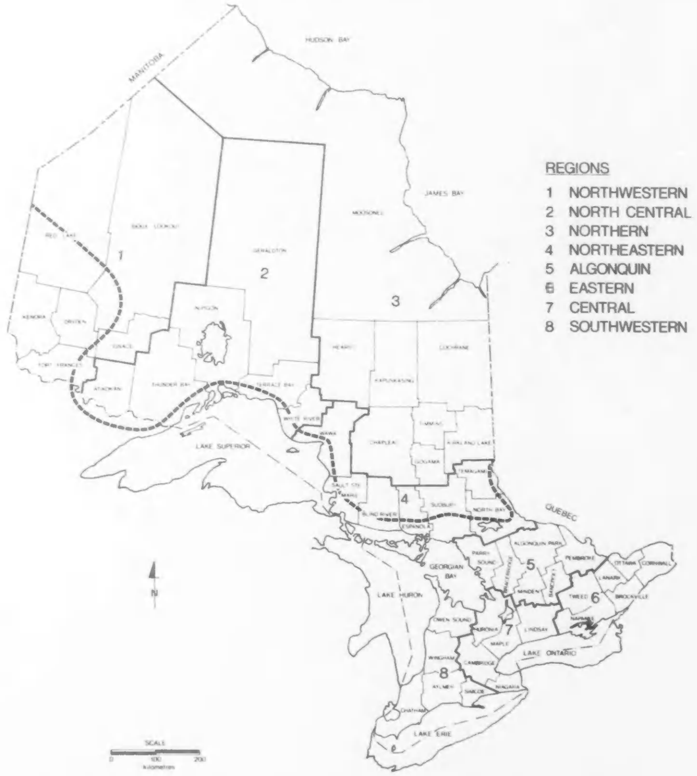
Discriminant analysis of data is presented which allows a partial classification of the lake types. A less rigorous procedure of classification utilizing climatological data and the zoogeographical distributions of the fish associations, in addition to the limnological information, is developed. A preliminary schema of lake types is presented.

The data have limitations, as discussed later, but we believe that this is the first attempt to analyze characteristics of a large sample of Ontario lakes including a range of walleye lakes from eutrophic to mesotrophic to oligotrophic lakes which have walleye as part of a more spatially complex association of walleye with lake trout.

Data Selection and Statistical Analysis

Two data sets were assembled initially for each of 3378 lakes in the lake inventory records. The first data set consisted of a coded list of the fish species present in each lake excluding the Cyprinidae, whose presence/absence was incompletely recorded for many lakes. In all, 58 species of fish were noted; the white sucker (*Catastomus commersoni* and the yellow perch (*Perca flavescens*) had the greatest frequencies. Note, however, that the selection criterion for inclusion in the sample, that the lake must be known to hold one or more of the four species named above, tended to give a distorted sample of the conditions that determine presence/absence of any one of the four species, since there are many Ontario lakes where none of these species is present. The second data set consisted of limnological variables (Table 1). Data were not available on all 11 variables for all of the lakes selected; only 440 lakes had data for all variables. Therefore, the data were examined first in toto to assess the degree of redundancy involved in the use of all variables. Oxygen, the least frequently recorded variable, was dropped from the analysis, leaving 2275 lakes where data on the remaining 10 variables were available. Area, mean depth, maximum depth, and shoreline development were transformed to natural logarithms to normalize their distributions. Principal component analysis was performed, following Lee (1971), which indicated that seven components would explain 96% of the variance. Three variables were identified from the orthogonalized principal components as being superfluous to any multivariate analysis of the data and were excluded. First, maximum depth ($\log_e$) and percent littoral were highly correlated with mean depth ($\log_e$) and contributed little directly to the sample variance. Second, total dissolved solids were highly correlated with alkalinity and contributed little to the sample variance. The frequency distributions of each of the seven remaining variables were examined more closely; the distributions of Secchi depth and alkalinity were more normal with logarithmic transformation of Secchi depth and reciprocal transformation of alkalinity. A final principle component analysis was performed on 2496 lakes with the seven variables to ensure that no further adjustments were necessary; results were essentially unchanged. These lakes were sorted into 15 groups (Table 2) representing the $2^4 - 1$ combinations of presence/absence of the four species.

Given that the 2496 lakes were classified a priori into 15 species associations, a canonical discriminant analysis was performed to assess the degree to which the species associations could be identified using linear functions of the seven limnological variables. Though the covariance matrices ($\chi^2 = 39033.25$ with 392 df) and class frequencies were not equal, the results were useful in developing a classification or schema of lake types. Mean depth ($\log_e$) and Secchi depth ($\log_e$) were the main factors in the first canonical equation (Table 3) and primarily distinguished lake trout lakes from non-lake trout lakes (Fig. 2); that is, the greater the mean depth and the greater the Secchi depth, the more likely the lake was to contain lake trout. Lake size (shoreline development and then area) was the main factor in the second canonical equation (Table 3), although Secchi depth exerted an important negative effect. This equation indicated a progression from simple to complex associations in the lake trout lakes, whereas for non-lake trout lakes the combinations of pike and/or bass with walleye were segregated from the others (Fig. 2). The third


HUDSON BAY
MANITOBA
JAMES BAY
1
2
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LAKE SUPERIOR
GEORGIAN BAY
LAKE HURON
LAKE ONTARIO
LAKE ERIE
QUEBEC
N
SCALE
0
100
200
kilometres
REGIONS
1 NORTHWESTERN
2 NORTH CENTRAL
3 NORTHERN
4 NORTHEASTERN
5 ALGONQUIN
6 EASTERN
7 CENTRAL
8 SOUTHWESTERN

FIG. 1. Regions and districts of the Ontario Ministry of Natural Resources. Broken line is 100-day frost-free period above 0°C (Chapman and Thomas 1968).

canonical equation was less readily interpreted but primarily segregated smallmouth bass lakes from those without bass.

TABLE 1. Summary of morphometric and limnological information on 3378 Ontario lakes used in present analysis.

Variable	No. of lakes	Min	Mean	Max
Area (ha)	3373	0.4	510.4	79771.7
Elevation (m)	3061	56.4	325.1	609.6
Mean depth (m)	3316	0.2	6.7	48.8
Max depth (m)	3368	0.6	20.8	185.9
% littoral[a]	3196	1.0	63.9	100.0
Shoreline development[b]	3257	1.0	2.6	12.9
Secchi disk (m)	3314	0.2	3.9	19.8
pH (minimum)	3081	3.9	6.7	9.5
Alkalinity (mg/ℓ)	3159	0.8	46.4	290.7
Total dissolved solids (mg/ℓ)	2917	4.7	58.0	462.7
Oxygen[c] (mg/ℓ)	655	0.0	5.0	11.2

[a] Percentage of lake area overlying water of a depth ≤6.1 m (20 ft).

[b] Shoreline length $(2\pi\sqrt{\text{area}/\pi})$.

[c] Average concentration where temperature was <15°C.

Geographic Distributions of Lake Types

Lake trout–smallmouth bass lakes — Lakes of this type occurred mainly in the six districts of the Algonquin Region in the Algonquin highlands, where 126 of the total of 152 lakes had these two species but neither pike nor walleye were found. Another 22 such lakes were found between Sault Ste. Marie and Temagami in the Northeastern Region. This was the second most frequent lake type (22% of survey lakes) in the Algonquin Region districts behind the lake trout "only" type in Algonquin Park District (67%) and the bass "only" type in the other five districts (23–44%) in the Region (Table 4).

Lake trout "only" lakes — These lakes (389) comprised 13% of the sample: 314 in the 13 districts of the Northeastern and Algonquin regions and 49 in 9 districts in northwestern Ontario

TABLE 2. Characteristics of 15 lake types and frequencies of occurrence. The following variables were used in discriminant analysis: $\log_e$ area, $\log_e \bar{z}$, $\log_e$ shore development, $\log_e$ Secchi depth, 100/alkalinity. Frequencies of z_{max}, % littoral, and TDS (total dissolved solids) data are slightly lower than frequencies of lake types because of some missing data. MEI was calculated as TDS divided by $\bar{z}$. I.D. means insufficient data, < 10 observations.

	Association	No.	Area (ha)	$\bar{z}$ (m)	Elevation (m)	z_{max} (m)	Littoral %	Shore dev.	Secchi depth (m)	pH min	Alkalinity (mg/l)	TDS (mg/l)	MEI (metric)	O_2 (mg/l)
1a.	LB	152	173	9.9	329	33.2	41.6	2.4	5.2	6.3	15.1	29.7	3.3	6.5
1b.	L	389	104	8.8	377	29.0	45.1	2.2	5.1	6.3	13.4	26.7	3.3	6.0
2a.	LWP	84	1120	11.9	368	47.4	39.0	4.0	4.2	6.6	20.1	33.0	3.1	6.7
2b.	LWPB	53	952	11.3	300	41.0	37.8	3.9	4.4	6.5	19.2	35.1	3.2	6.3
3a.	LP	92	382	10.8	391	39.1	39.0	2.9	4.4	6.7	19.7	36.5	3.9	6.6
3b.	LPB	37	410	11.3	279	40.8	36.6	3.4	5.2	6.5	16.6	44.6	4.3	6.8
4.	B	259	36	3.9	319	12.5	71.5	1.8	3.5	6.5	19.8	63.5	28.0	2.9
5a.	P	476	37	3.1	333	12.1	78.3	1.9	2.7	6.9	30.4	72.2	31.8	3.8
5b.	PB	87	96	4.5	224	15.5	64.1	2.2	3.3	7.0	29.0	111.5	49.8	2.9
6.	W	47	66	3.8	316	12.9	71.9	1.9	2.9	6.7	20.0	57.6	19.3	I.D.
7a.	WP	553	244	3.5	340	14.1	77.0	2.5	2.4	7.0	31.3	57.2	20.6	4.2
7b.	WPB	178	249	5.0	280	17.8	65.1	2.9	3.1	6.6	25.5	58.2	14.5	3.9
8.	WB	68	241	4.1	272	15.0	67.8	2.5	3.3	6.6	21.5	66.8	26.9	I.D.
Rare	LW	15	271	12.5	383	41.9	38.9	3.1	5.3	6.4	16.8	32.8	3.1	I.D.
Rare	LWB	17	322	10.5	316	38.4	38.4	2.9	5.8	6.3	16.3	39.2	4.0	I.D.

TABLE 3. Results of discriminant analysis on 15 associations. Significant values are underlined.

	Canonical roots			
Statistics	1	2	3	4
Root	0.951	0.743	0.493	0.216
χ^2	3401.675	1800.354	707.644	167.659
df	98	78	60	44
Canonical coefficients				
Area ($\log_e$)	−0.125	$\underline{0.427}$	0.022	−0.165
Elevation	0.001	0.002	−0.009	−0.000
Mean depth ($\log_e$)	$\underline{-0.980}$	0.095	$\underline{-0.263}$	0.307
Shoreline development ($\log_e$)	0.068	$\underline{0.567}$	0.028	0.462
Secchi depth ($\log_e$)	$\underline{-0.957}$	$\underline{-0.468}$	$\underline{0.493}$	−0.087
pH	0.074	0.173	$\underline{-0.360}$	0.252
100/alkalinity	−0.096	−0.052	0.007	−0.024

from the Nipigon District west. Approximately two thirds of sampled lakes in the Sault Ste. Marie, Blind River, and Algonquin Park districts were lake trout "only" lakes, but only about 7% of the lakes in northwestern Ontario (Nipigon District west) were of this type.

Lake trout–walleye–pike lakes — A large majority of this type, 70 of 84 lakes with this species combination occurred in northwestern Ontario from the Nipigon District west. Five others were present in the Temagami District. Approximately 10% of the lakes in northwestern Ontario were of this type.

Lake trout–walleye–pike–smallmouth bass lakes — This type was relatively uncommon, occurring in 53 lakes altogether, dispersed in 19 lakes through the districts from Nipigon west and in 30 lakes in districts from Blind River east to Temagami, North Bay, and Parry Sound, plus 4 other lakes. In Temagami and North Bay districts 12 and 16%, respectively, were of this type but its relative frequency was much less elsewhere.

Lake trout–pike lakes — A total of 92 lakes were of this type: 62 in northwestern Ontario from the Nipigon District west, 28 scattered in 13 districts eastward to Sudbury and North Bay districts, and 2 farther south. Approximately 10% of the northwestern Ontario lakes were of this type.

Lake trout–pike–smallmouth bass lakes — Only 37 lakes were of this type: 10 in four northwestern districts (Sioux Lookout, Kenora, Fort Frances, and Atikokan), 22 in six districts from Blind River east to Temagami, North Bay, and Parry Sound, and 5 in southeastern Ontario.

Smallmouth bass "only" lakes — This common type comprised 259 lakes. The majority, 184 lakes, were in the Algonquin Region; about 40% of Bracebridge, Bancroft, and Minden district

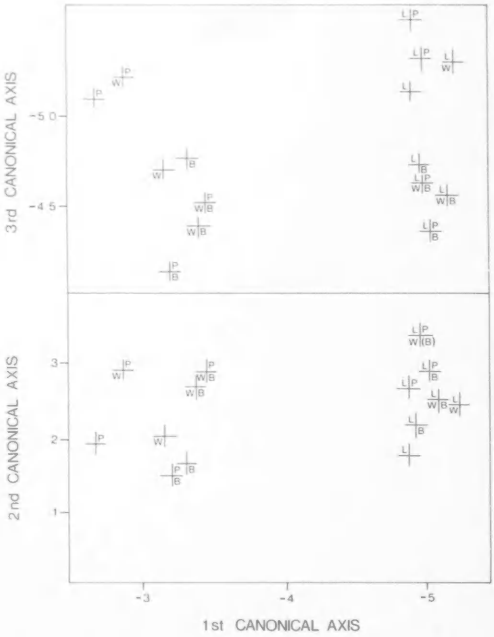

FIG. 2. Centroids of the 15 fish associations on the first three canonical axes. See text for description of statistical method employed.

lakes, about 25% of Pembroke and Parry Sound lakes, and 13% of Algonquin Park lakes. Of the rest, 48 were scattered throughout 10 districts in southern Ontario, 27 were north and west of North Bay (16 in the 5 districts from North Bay to Sault Ste. Marie), and 6 in northwestern Ontario in Nipigon, Thunder Bay, and Atikokan districts.

Pike "only" lakes — The second most abundant lake type (476 lakes in total compared with 553 walleye–pike lakes) occurred in 196 lakes in the five "claybelt" districts of northern Ontario (Hearst, Kapuskasing, Cochrane, Timmins, and Kirkland Lake), in an additional 98 lakes in northern Ontario and in 122 lakes in northwestern Ontario from the Nipigon district west. A large number of these lakes occurred in southern Ontario: 22 in the Eastern Region and 22 in the South-Central and Southwestern regions. None occurred in Algonquin, Bracebridge, and Minden districts, and only one in the Bancroft district. These four districts comprise the Algonquin highlands where the pike is rare or, in some large areas, absent. The Parry Sound and Pembroke districts had 15 pike "only" lakes at lower elevations to the west and east of the Algonquin highlands. This lake type was relatively common in many districts, 45, 29, and 25% of lakes in the Thunder Bay, Nipigon, and Terrace Bay districts, 33–66% in the five "claybelt" districts, 76% in the Chapleau district, about 25% in Gogama and Sudbury district lakes, and 23–36% in Brockville, Lanark, Huronia, Maple, Cambridge, Wingham, and Aylmer districts in southern Ontario.

Pike–smallmouth bass lakes — A large proportion of the 87 lakes in this group occurred in three locations: 37 lakes in southeastern Ontario, 12 lakes in the Owen Sound District, and 25 in six districts from Blind River east and northeast to North Bay and Kirkland Lake. Of the remaining 13, 6 were in northwestern Ontario and 7 in other southern Ontario districts. This was the predominant type in Brockville, Napanee, and Owen Sound districts with 37, 48, and 33% of lakes, respectively.

Walleye "only" lakes — This small group of 47 lakes was scattered throughout Ontario from the Red Lake District to the Lanark District. Ten such lakes comprised 6% of lakes in the Kirkland Lake District.

Walleye–pike lakes — This, the commonest group of lakes, totaled 553, of which 535 occurred north of and including Wawa, Chapleau, Gogama, and Temagami districts. Most lakes were of this type in the following districts: Red Lake (53%), Sioux Lookout (66%), Geraldton (72%), Terrace Bay (51%), White River (75%), Hearst (67%), and Cochrane (51%). In addition, this was the commonest lake type in Dryden, Ignace, Fort Frances, Atikohan, and Nipigon districts (26–42%).

Walleye–pike–smallmouth bass lakes — The 178 lakes in this group included 58 lakes in northwestern Ontario, 56 in seven districts from Espanola, Gogama, and Kirkland Lake south to Parry Sound and Bracebridge and 42 in six districts from Pembroke south to Napanee and Brockville. This was the commonest lake type in the Kenora, Lanark, and Tweed districts, at 28, 32, and 43% of lakes, respectively.

Walleye–smallmouth bass lakes — This type (68 lakes) was of significant occurrence (55 lakes) in six districts, North Bay south through Parry Sound, Bracebridge, Minden, and Bancroft to Lindsay. Only six lakes in northwestern Ontario had this association. All of the 16 lakes in the Lindsay district were of this type; North Bay and Minden were closest in relative frequency with only 13% and 10% respectively.

Rare types — There were 15 lake trout–walleye lakes, 9 of them in northwestern Ontario. Also, lake trout–walleye–smallmouth bass associations were found scattered through 17 lakes in 12

TABLE 4. Distributions of lake types by districts as percentages of number of lakes in each district. Based on 2484 lakes, districts with < 10 lakes surveyed having been omitted. Percentage frequencies < 10% are shown as +.

District	No. lakes	LB	L	LWP	LWPB	LP	LPB	B	P	PB	W	WP	WPB	WB
Red Lake	40	—	+	25	—	10	—	—	—	—	+	53	+	—
Sioux Lookout	67	—	+	+	+	+	+	—	13	—	—	66	+	—
Kenora	98	+	+	+	+	+	+	—	11	+	—	26	28	+
Dryden	53	–	23	+	+	+	–	–	11	+	+	36	+	+
Ignace	50	–	+	10	+	+	–	–	12	–	+	42	14	–
Fort Frances	65	–	+	15	+	12	+	–	12	–	–	40	+	–
Geraldton	81	–	–	+	–	+	–	–	14	–	+	72	–	–
Nipigon	62	–	+	+	–	11	–	+	29	–	+	39	+	–
Atikokan	111	–	+	17	+	11	+	+	14	+	+	26	12	+
Terrace Bay	53	+	11	–	–	+	–	–	25	–	+	51	–	–
Thunder Bay	110	–	11	+	+	13	–	+	45	+	+	23	+	–
White River	44	–	+	+	–	+	–	–	14	–	–	75	–	–
Hearst	36	–	–	–	–	–	–	–	33	–	–	67	–	–
Kapuskasing	43	–	+	–	–	–	–	–	49	–	+	42	–	–
Cochrane	92	–	+	+	–	+	–	–	43	–	–	51	–	–
Timmins	66	–	+	–	–	+	–	+	65	–	–	27	–	–
Chapleau	46	–	–	–	–	+	–	+	76	–	–	20	–	–
Kirkland Lake	158	–	+	+	–	+	–	+	51	+	+	29	+	+
Gogama	21	–	19	+	+	–	–	10	24	10	10	19	–	–
Wawa	51	–	39	+	–	+	–	–	10	–	+	29	–	–
Temagami	84	+	32	+	12	+	+	+	+	+	+	+	19	–
Sault Ste Marie	65	12	71	–	–	–	–	+	+	–	+	–	+	+
Blind River	77	+	66	–	+	+	+	+	+	+	–	–	–	–
Sudbury	45	+	+	–	+	+	+	+	27	20	+	+	13	–
North Bay	45	+	22	–	16	+	+	+	+	+	+	+	16	13
Espanola	45	+	29	–	+	+	+	16	+	+	–	–	16	–
Algonquin Park	126	17	67	–	–	–	–	13	–	+	–	–	–	–
Pembroke	47	13	+	–	+	+	–	23	19	+	+	–	17	+
Parry Sound	91	20	+	+	+	–	+	25	+	+	+	+	19	+
Bracebridge	135	20	22	–	–	–	–	44	–	+	+	–	+	+
Bancroft	86	29	+	–	–	+	+	42	+	+	+	+	+	+
Minden	97	30	20	–	–	–	–	38	–	–	+	–	–	10
Lanark	31	–	+	–	–	–	–	10	23	16	+	10	32	+
Brockville	27	–	–	–	+	–	+	–	33	37	–	–	19	–
Tweed	28	–	–	–	–	–	–	18	18	+	–	11	43	–
Napanee	25	+	–	–	–	–	+	20	–	48	–	–	20	–
Huronia	15	–	–	–	–	–	–	13	27	13	+	13	27	–
Lindsay	16	–	–	–	–	–	–	–	–	–	–	–	–	100
Maple	11	–	–	–	–	–	–	64	36	–	–	–	–	–
Cambridge	11	–	–	–	–	–	–	45	27	+	+	–	+	+
Owen Sound	30	–	–	–	–	–	–	30	13	33	–	+	10	+

districts, 3 in Atikokan and Kenora and the remainder in 10 districts from Blind River east to Temagami and south to Bancroft.

Schema of Lake Types

The relative importance of lake characteristics, derived by discriminant analysis, together with zoogeographic considerations, permitted development of a schema of lake types (Fig. 3). The main factors used in this schema are lake depth, which distinguished lake trout from non-lake trout lakes with fair precision, and lake area, which was used in both groups to segregate small lakes with one or two of the species. Further breakdown was achieved, with a great deal less reliability, using TDS and Secchi depth. Final breakdown was made generally on the basis of climate as it affects the distribution of smallmouth bass. This species is distributed northward in Ontario not much farther than the July mean temperature of 18°C or the mean annual frost-free period (above 0°C) of 100 days (Fig. 1). Year-class strength has been positively related to accumulated temperature experience of the fish in their first summer (Fry and Watt 1955).

Discussion

Most lakes with lake trout differed from non-lake trout lakes in several respects. The former

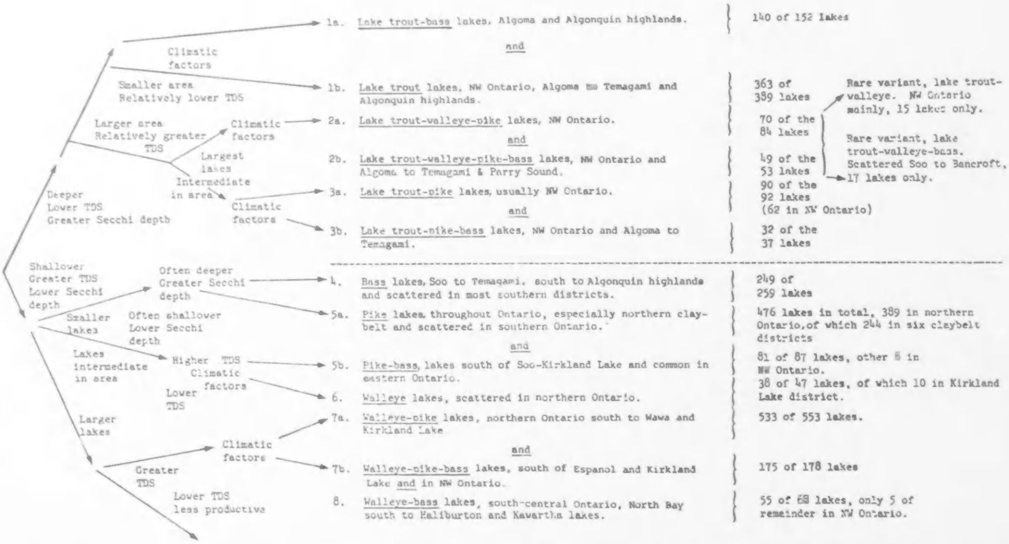
Climatic factors
Smaller area
Relatively lower TDS
Larger area
Relatively greater TDS
Climatic factors
Largest lakes
Intermediate in area
Climatic factors
Deeper
Lower TDS
Greater Secchi depth
Shallower
Greater TDS
Lower Secchi depth
Often deeper
Greater Secchi depth
Smaller lakes
Often shallower
Lower Secchi depth
Lakes intermediate in area
Higher TDS
Climatic factors
Lower TDS
Larger lakes
Climatic factors
Greater TDS
Lower TDS
less productive
1a. Lake trout-bass lakes, Algoma and Algonquin highlands.
140 of 152 lakes
and
1b. Lake trout lakes, NW Ontario, Algoma [illegible] Temagami and Algonquin highlands.
363 of 389 lakes
Rare variant, lake trout-walleye. NW Ontario mainly, 15 lakes only.
2a. Lake trout-walleye-pike lakes, NW Ontario.
70 of the 84 lakes
and
2b. Lake trout-walleye-pike-bass lakes, NW Ontario and Algoma to Temagami & Parry Sound.
49 of the 53 lakes
Rare variant, lake trout-walleye-bass. Scattered Soo to Bancroft, 17 lakes only.
3a. Lake trout-pike lakes, usually NW Ontario.
90 of the 92 lakes (62 in NW Ontario)
and
3b. Lake trout-pike-bass lakes, NW Ontario and Algoma to Temagami.
32 of the 37 lakes
4. Bass lakes, Soo to Temagami, south to Algonquin highlands and scattered in most southern districts.
249 of 259 lakes
5a. Pike lakes, throughout Ontario, especially northern clay-belt and scattered in southern Ontario.
476 lakes in total, 389 in northern Ontario, of which 244 in six claybelt districts
and
5b. Pike-bass, lakes south of Soo-Kirkland Lake and common in eastern Ontario.
81 of 87 lakes, other [illegible] in NW Ontario.
6. Walleye lakes, scattered in northern Ontario.
38 of 47 lakes, of which 10 in Kirkland Lake district.
7a. Walleye-pike lakes, northern Ontario south to Wawa and Kirkland Lake
533 of 553 lakes.
and
7b. Walleye-pike-bass lakes, south of Espanol and Kirkland Lake and in NW Ontario.
175 of 178 lakes
8. Walleye-bass lakes, south-central Ontario, North Bay south to Haliburton and Kawartha lakes.
55 of 68 lakes, only 5 of remainder in NW Ontario.

FIG. 3. Schema of relationships of 15 fish associations to limnological characteristics of Ontario lakes. Frequencies and geographic distributions of lake types are amplified in text.

had greater mean depth and Secchi transparency and lower total dissolved solids, the first two variables being most meaningful in discriminant analysis. Most lake-trout lakes exceeded 6 m in mean depth and most non-lake trout lakes had mean depth <6 m. For example, for three common lake types of the Algonquin Region, 113 of 146 lake trout "only" lakes and 107 of 124 lake trout–smallmouth bass lakes had mean depth >6 m, and 146 of 181 bass "only" lakes were <6 m in mean depth. Total dissolved solids of 50 mg/ℓ appeared to maximize separation of lake trout and non-lake trout lakes but a considerable overlap still occurred. A morpho-edaphic index (MEI of Ryder 1965) of 6 appeared to separate lake trout from non-lake trout lakes. Lake trout "only" and lake trout-bass lakes had average hypolimnetic dissolved oxygen of 6.0 and 6.5 mg/ℓ, but bass "only," pike "only," walleye–pike and walleye–pike–bass lakes averaged 2.9, 3.8, 4.2, and 3.9 mg/ℓ. These oxygen concentrations were related to mean depth, as expected, because deeper hypolimnia of greater volume have a greater absolute supply of oxygen at onset of thermal stratification.

The larger lake trout lakes usually contained walleye and pike or both of these species plus smallmouth bass. Characteristics of these lakes with and without bass were similar (Table 2). Such lakes with bass in northwestern Ontario were originally lake trout–walleye–pike lakes, and many of the lakes there apparently remain without bass because the species was not introduced or did not always succeed when introduced. Such is also the case in the area from Blind River to Temagami (excluding the North Bay District, which had some native smallmouth bass populations), although it appears that introductions of bass to extend its range were apparently more effective to the north of North Bay than in northwestern Ontario. At least this is implied by the difference between regions in percentages of the trout–walleye–pike lakes with bass and without bass.

The two rare species combinations (the lake trout–walleye combination in 15 lakes and these two species plus smallmouth bass in 17 lakes) were so infrequent as to suggest that pike might have been present but not taken in the sampling program. If, in fact, pike were absent, possibly these lakes lacked extremely shallow areas required for spawning by pike. The absence of pike can be explained on zoogeographic grounds for only a minority of these lakes in the Algonquin highlands, an area the species has not effectively colonized. The average size of these 32 lakes where pike are "missing" was less than the average size of trout–walleye–pike and trout–walleye–pike–bass lakes, but they were similar in other characteristics and were similarly distributed. All of these types where lake trout and walleye occur together (with or without pike and/or bass) had low MEI, averaging about 3, compared with the average MEI of 14 in the two common types of lakes, walleye–pike and walleye–pike–bass. Of the

169 lakes with lake trout and walleye, 81% contained pike and 32% had bass as well. Although this is a small proportion of the total sample, these lakes are of considerable significance by virtue of their usual large area and accessibility.

The smaller lake trout lakes are most likely to be in the lake trout "only" or lake trout–bass categories. Their locations in Algoma (Sault Ste. Marie and Blind River districts), Temagami District, and the Algonquin highlands of the Algonquin Region were similar in terms of high local elevation, steep drainage systems, and edaphic oligotrophy. These lakes were much less likely to sustain percid communities even if colonization had been promoted through stocking programs. The smallmouth bass, on the other hand, was native to many of these lakes and was probably stocked in many others, especially in the Bracebridge, Minden, and Bancroft districts. A few of the lakes in Algoma and Temagami, which were at one time lake trout "only" lakes, have sustained smallmouth bass after stocking. The lake trout "only" and lake trout–bass lakes were similar (Table 2); together they numbered 541 lakes, or 22% of the sample. Many are in prime recreational areas, easily accessible within half a day's drive of large metropolitan areas and are subject to heavy fishing in relation to low productivity implied by low MEI. These two types had very low average MEI. Apparently no hard evidence exists that demonstrates that smallmouth bass are detrimental to lake trout populations. A common characteristic of bass populations is heavy utilization of crayfish (McKay 1963), which are not common in the diet of lake trout.

Lake trout–pike and lake trout–pike–bass lakes were similar in most respects to those that also had walleye, except that the average area was considerably less. Of the 129 lakes of the two types, nearly a third had smallmouth bass, mainly by introductions by man; only 10 of the 37 lakes occurred in the native range of the species. Many more lake trout–pike lakes must have been stocked with bass than have sustained them, as indicated by only 10 lake trout–pike–bass lakes in northwestern Ontario compared with 63 lake trout–pike lakes.

The obvious question is why walleye did not occur in the many lakes (129) of the lake trout–pike and lake trout–pike–bass types, spread across the same broad band of districts (from Red Lake to Parry Sound) as the lakes that had walleye together with pike and often bass. This was essentially the same broad band in which almost all 553 walleye–pike lakes occurred, which were smaller lakes, on the average, than the lake trout–pike lakes. Size of lake, per se, may not be important. However, the smaller walleye–pike lakes had greater average total dissolved solids and lower mean depth (Table 2). The MEI, consequently, averaged more than 5 times as great in the walleye–pike lakes as in the lake trout–pike lakes (20.6 compared with 3.9). Since low MEI has not excluded walleye from large lake trout lakes, the data suggest a combined effect of lake area and MEI on success of walleye. A small, low-MEI lake may be less suitable for walleye than a large, low-MEI lake. Larger lakes, with low overall MEI, can have higher MEI bays which could be as large as smaller, high-MEI lakes. This appears to be a more useful hypothesis than, for example, the absence of spawning areas, which is one possible explanation for the occasional absence of pike in lakes with lake trout. This is based on the simple premise that lakes that have rocky shoals and littoral zones satisfactory for lake trout are expected to meet the spawning requirements for shoal-spawning walleye. Another factor is the possibility for greater success of walleye in small interconnected lakes in areas of flat relief, than in small lakes, poorly connected, in areas of rugged relief. Carlander (1977) noted the presence of walleye in large lakes and in interconnected small lakes and implied the need for "Lebensraum" of sorts.

Discussion to this point has dealt with low MEI lakes with lake trout and possible combinations with the other three species. Only 169 of 839 lakes with lake trout (20%) also had walleye. These often seemed to be the larger lakes, which are more likely to contain suitable walleye habitat of sufficient magnitude. In simplest terms, a large oligotrophic lake is more likely to have mesotrophic environments of sufficient scope for percids than a small oligotrophic lake. In general, large lakes have greater diversity of habitat. These Ontario data support findings of Barbour and Brown (1974) that lake area is a prime determinant of the number of fish species in lakes. Caution should be applied, therefore, in the use of individual MEI data for large, complex lakes.

The shallower lakes, richer in total dissolved solids and with MEI usually in excess of 10, had a greater frequency of walleye than lake trout lakes (54% of 1688 lakes compared with 20% of 839 lakes). Pike had a higher frequency of occurrence (78% compared with 33% of lake trout lakes), while the smallmouth bass was nearly equally associated with the two types (36% compared with 32% in lake trout lakes).

Two of the most frequent lake types, with the smallest average area of 36–37 ha, were the pike "only" and smallmouth bass "only" types. Characteristics of the two types were very similar; bass lakes were about 1 m greater in mean depth and Secchi depth but the overlap was extensive. The pike–bass lakes were larger, at 96 ha, than the pike and bass "only" and they were not as numerous as the latter types. This suggests that competition and predation between the two species minimizes the probability of coexistence in small lakes. In larger lakes the coexistence of bass and pike was common, as in 178 walleye–pike–bass lakes which averaged 249 ha in area. The walleye–pike and pike "only" types were similar in mean depth but the former were several times larger on average. MEI tended to be greater in pike lakes (31.8) than in walleye–pike lakes (20.6).

Lake area (Table 5) was the only gross characteristic that shed some light on the question of why pike "only" lakes do not have walleye. Probably a variety of factors may be significant from lake to lake, not the least of which is the spawning requirements of walleye. Possibly larger lake area permits sufficient wave action to expose boulder and gravel substrate for walleye spawning. "Lebensraum" may be a requirement per se, or else pike and walleye coexistence may have lower probability of success in smaller lakes.

Of the 178 walleye–pike–bass lakes in the sample, slightly over 100 probably contained smallmouth bass through introductions; the balance in the area of Georgian Bay and in southeastern Ontario most likely were native associations. There was no apparent difference in walleye–pike lakes with and without smallmouth bass in Ontario, other than location, reflecting the northward extension of the range of the smallmouth bass to Kirkland Lake in the northeast and in much of northwestern Ontario. A third lake type with walleye present is the walleye–bass type, represented by 68 lakes. Only five occurred in northwestern Ontario and pike might have been missed in sampling these lakes. However, in south–central Ontario, specifically in the Bancroft, Minden, and Lindsay districts, pike probably were not present. In 27 lakes muskellunge were present, making these lakes walleye–esocid–bass lakes and leaving only 41 walleye–bass lakes, mostly between Bracebridge and North Bay. The walleye–pike lakes (553), walleye–pike–bass lakes (178), and the walleye–bass lakes (68) comprised the bulk of lakes with walleye that had high MEI values, 20.6, 14.5, and 26.9, respectively, compared with MEI of about 3 in lake trout lakes with walleye. Characteristics of these 799 lakes were as follows: area, 245 ha; mean depth, 3.9 m; shore development, 2.62; Secchi disc transparency, 2.6 m; alkalinity, 28.7 mg/ℓ; total dissolved solids, 58.4 mg/ℓ; MEI, 19.5.

TABLE 5. Frequency distributions by lake area (in intervals) for walleye "only", pike "only," and pike-walleye lakes in all districts.

Intervals in area (ha)	Walleye "only"	Pike "only"	Pike and walleye
0.4– 1.4	0	2	0
1.4– 4.6	2	38	1
4.6– 15.6	4	98	12
15.6– 52.7	14	150	59
52.7– 178.7	18	119	160
178.7– 605.4	8	50	187
605.4– 2051.0	1	16	90
2051.0– 6949.3	0	2	34
6949.3–23600.0	0	0	7
23600.0–80000.0	0	0	2

The remaining lake type is walleye "only," of which only 47 occurred in the sample. They tended to be smaller lakes on average than the walleye–pike lakes, 66 ha compared with 244 ha, but they were of approximately the same size (Table 5) as pike "only" lakes, suggesting that either pike were missed or these walleye "only" lakes lacked suitable spawning areas for pike. They were wisely dispersed through 24 districts, and only four lakes had muskellunge (*Esox masquinongy*).

Many factors remain unconsidered; however, several hypotheses are implicit in the present analysis. For example, hypotheses to explain the low frequency of walleye in small lakes include possibilities of (1) low probability of successful coexistence of pike and walleye in small lakes, (2) lack of wind fetch in small lakes to clear spawning areas, and (3) "Lebensraum" requirement of the walleye.

More intensive data on selected lakes would permit testing of these and other relevant hypotheses, and, in addition, would provide the foundation for experimental management based on selected, representative lake sets. Three factors were not considered in the derivation of this data set. First, recording of the mere presence/absence of fish species lumps together lakes ranging in conditions from those where the species is of minor abundance to those where it achieves its greatest production. The inclusion of variables reflecting the performance of the species (e.g. relative abundance, growth) would have greatly improved the chances of securing an objective limnological classification. Secondly, ecological groups of fish species can be considered as interchangeable in designating a class of lakes, for example, esocid lakes rather than just northern pike lakes, or salmonid lakes rather than just lake trout lakes. Allowing such "substitutions" might result in some redistribution of fish association frequencies. Thirdly, morphometry dominated the classification criteria in the discriminant analysis, and an extension of the limnological data set to include variables that more directly reflect the productivity of the lakes would improve the classification.

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Biomass, Production, and Yields of Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*) in North American Lakes[1,2]

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CARLANDER, K. D. 1977. Biomass, production, and yields of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in North American lakes. J. Fish. Res. Board Can. 34: 1602–1612.

Compilation of available data indicated that walleye (*Stizostedion vitreum vitreum*) biomass in lakes averaged 16 kg/ha, but the data were not adequate to show relationships with mean depth, alkalinity, latitude, or morphoedaphic indexes of the lakes. Yellow perch (*Perca flavescens*) biomass also failed to show relationships with these factors. In small lakes and ponds with only perch, biomass ranged from 39 to 215 kg/ha, but in lakes with other species, perch biomass was under 65 kg/ha. Annual production of walleye was from 1.2 to 4.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ and that of yellow perch was 21.9 $kg \cdot ha^{-1} \cdot yr^{-1}$. Average commercial yields of walleye ranged up to 3.06 $kg \cdot ha^{-1} \cdot yr^{-1}$, and sport fish yields averaged 3.7 $kg \cdot ha^{-1} \cdot yr^{-1}$. Annual commercial and sport yields decreased with latitude. Area of lake was negatively correlated with sport yield, but positively with commercial yield. The latter situation is believed to be an artifact of the sample and not a general trend. Commercial yield increased with total dissolved solids of the lakes. Lack of other correlations may be related to the fact that walleye biomass and yield do not bear a constant relationship to total biomass and yield.

Key words: Percidae, *Stizostedion*, *Perca*, biomass, production, yield

CARLANDER, K. D. 1977. Biomass, production, and yields of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in North American lakes. J. Fish. Res. Board Can. 34: 1602–1612.

Une compilation des données disponibles indique que la biomasse des dorés jaunes (*Stizostedion vitreum vitreum*) dans les lacs était en moyenne de 16 kg/ha, mais ces données sont insuffisantes pour montrer les relations avec la profondeur moyenne, l'alcalinité, la latitude ou les indices morphoédaphiques des lacs. La biomasse des perchaudes (*Perca flavescens*) ne montre pas, elle non plus, de relations avec ces facteurs. Dans les petits lacs et les étangs ne contenant que des perchaudes, la biomasse varie de 39 à 215 kg/ha, mais dans les lacs contenant d'autres espèces, la biomasse des perchaudes est inférieure à 65 kg/ha. La production annuelle de dorés jaunes varie de 1.2 à 4.1 $kg \cdot ha^{-1} \cdot a^{-1}$, et celle des perchaudes est de 21.9 $kg \cdot ha^{-1} \cdot a^{-1}$. Les rendements commerciaux moyens en dorés jaunes vont jusqu'à 3.06 $kg \cdot ha^{-1} \cdot a^{-1}$, et les rendements de la pêche sportive sont en moyenne de 3.7 $kg \cdot ha^{-1} \cdot a^{-1}$. Les rendements commerciaux et sportifs diminuent tous deux en fonction de la latitude. Il y a une corrélation négative entre la superficie du lac et le rendement de la pêche sportive, mais une corrélation positive avec le rendement commercial. On croit que cette dernière situation est une erreur systématique d'échantillonnage plutôt qu'une tendance générale. Le rendement commercial augmente avec les solides totaux dissous des lacs. Il se peut que l'absence d'autres corrélations soit liée au fait que la biomasse et le rendement des dorés jaunes ne comportent pas de relation uniforme avec la biomasse et le rendement totaux.

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EVEN though information on production of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) would be helpful in management of the resources, few data are available. Data on 136 populations of walleye or yellow perch in North American lakes were compiled from a search of published, and some unpublished, reports. These data were reported as biomass, production, and yield.

Biomass, or standing crop, is weight of the population at any specified time. It is the result of the previous production, as affected by natural and fishing mortality. It is also somewhat a mea-

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Journal Paper No. J-8699 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa.

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sure of the productivity, or carrying capacity, of the environment. As biomass approaches carrying capacity net production (addition to biomass) decreases. Production is the tissue elaborated by the organisms through reproduction or individual growth within a specified period, whether or not that tissue survives to the end of the period. Yield means the number or weight of the organisms harvested from the population within a specified period of time.

For comparative purposes in this paper, these measures are expressed as kilograms per hectare (and per year for yield and production).

Biomass

Biomass is usually estimated by mark-and-recapture methods or by draining or chemical treatment of a lake or pond to recover all of the fish. Well-balanced, healthy populations are rarely estimated by chemical treatment. Mark and recapture usually is limited to fish above a given size; thus, the estimates do not include the younger fish. Biomass may also be estimated by determining numbers or weight of fish per area with gear that effectively captures all the fish in a given area; but gear is rarely consistent or effective in enough areas to adequately determine biomass in a lake.

Walleye — Comparatively few estimates of walleye biomass (Table 1) were found, and most of them do not apply to typical walleye lakes. Walleyes are most abundant in large unstratified lakes where the annual growing season has 500–720 degree-days above 12.8°C (Schneider 1973a).

In the three lakes with <3.3 kg/ha, walleye were not the principal predators. The lake trout, *Salvelinus namaycush*, was the major predator in Nipigon Bay; the northern pike, *Esox lucius*, in Burnt Camp Lake; and the smallmouth bass, *Micropterus dolomieu*, in East Twin Lake. Long Lake, with a biomass of 3.9 kg/ha, originally was noted as a smallmouth bass lake.

Biomass in the other lakes ranged from 5.7 to 37.0 kg/ha and the mean was 16.0, considering only the estimates for walleye longer than 300–350 mm. The three lakes under 100 ha had 18.7–37.0 kg/ha with a mean of 26.8; the nine lakes between 100 and 1000 ha, 6.1–15.5 kg/ha with a mean of 10.5; and the seven lakes over 1000 ha, 5.7–37.0 kg/ha with a mean of 18.4. The correlation between area and biomass was only 0.385 ($P > .05$), even eliminating the lakes <100 ha.

Correlation of biomass with mean depth of the lakes with latitude or length of growing seasons was not evident. The three Canadian lakes had a lower mean biomass, 8.2 kg/ha, than the eight Michigan, Minnesota, and Wisconsin lakes at 17.1 kg/ha and the eight Iowa, Ohio, and New York lakes at 17.3 kg/ha; but this is not sufficient to show latitudinal effects. There also is no evidence of correlation with alkalinity or with the morphoedaphic index, MEI (Ryder et al. 1974).

Standing crops within a lake change from year to year and from season to season as the result of harvest, reproductive success, and environmental changes. The estimates also have sampling variation even if there were no changes in biomass. For example, the range in estimated biomass was 1.65 times the mean of 27 annual estimates in Clear Lake, 1.35 times the mean of 16 annual estimates in Escanaba Lake, 0.92 times the mean of 6 annual estimates in Wilson Lake, and 0.52 times the mean of 5 estimates in 1 yr in West Blue Lake (citations as in Table 1).

Yellow perch — More biomass estimates (Tables 2–4) were found for perch than for walleye, but only three of those found were for percid lakes, or lakes in which walleyes were the major predator: Storm Lake, Iowa, with 7 kg perch/ha; East Twin Lake, Michigan, with 22 kg/ha; and Oneida Lake, New York, with 36 kg/ha.

The data from the other lakes do not add to our knowledge of percid lakes but give some information on perch populations. They are considered in three categories. The first (Table 2) is for lakes in which perch were < 20% of the fish biomass. Other estimates in which perch were a minor part of the population are available, but this listing includes most estimates in which perch were at least 2 kg/ha. In lakes in which perch were at least 20% of the fish biomass, the mean biomass of perch was 27 kg/ha (Table 3). Several of the lakes in both these lists were chemically treated because they contained undesirable populations of stunted perch, and the results from these lakes are thus not representative of lakes as a whole.

Most of the lakes are too shallow for the morphoedaphic indexes to be meaningful, and the data gave no indication of correlation between alkalinity and the biomass.

There are standing crop estimates for several ponds and small lakes in which yellow perch were the only species of fish (Table 4), and these ranged from 39 to 215 kg/ha. The biomass in some experimental ponds in Illinois (Buck and Thoits 1970) were 2–3 times as high as those of smallmouth or largemouth bass (*M. salmoides*) populations in the same ponds in other years.

Production

Annual production is the most meaningful measure of a population's response to the environ-

TABLE 1. Biomass (kg/ha) of walleye, other predators, and all fish in 23 North American Lakes, arranged according to increasing biomass.

Lake and citation	Area (ha)	Mean depth (m)	TDS (ppm)	MEI	Biomass		
					Walleye	Other predators	All species[a]
Nipigon Bay, Ont. Ryder 1968	34,200	10.8	71	7	1.1	—	—
East Twin, Wis. O'Donnell 1943	5	3.0	28[b]	9	2.3[c]	3.9	208
Burnt Camp, Minn. Maloney 1956	4	5.0	45	9	2.8	7.8	142
Long, Wis. O'Donnell 1943	11	3.0	76[b]	79	3.9[c]	0	151
West Blue, Man. Kelso and Ward 1972, 1977	162	11.3	18	16	6.1	—	—
Clear, Iowa Carlander and Payne 1977	1,474	3.6	230	64	5.7 7.2(age I+)	—	—
Dexter, Ont. Moenig 1975	368	1.8	—	—	7.2	—	—
Cadillac, Mich. Schneider 1973a	465	3.3	100[b]	30	8.2[d]	1.6[d]	28
East Okoboji, Iowa Rose 1957	764	2.8	272[b]	97	9.9[d]	—	—
Clear, Iowa McCann and Carlander 1970	1,474	3.6	230	64	10.4[d]	0.6	80
Many Points, Minn. Olson 1958	694	9.1	168	18	11.0[d]	—	—
Savanne, Ont. P. J. Colby personal communication 1975	364	2.6	65	25	11.2	8.5	—
Escanaba, Wis. Kempinger et al. 1975	119	4.3	43	10	12.3	6.0	—
Spirit, Iowa Jennings 1968, 1969, 1970 Moen 1963, Rose 1955, 1957	2,168	5.2	271[b]	52	12.4[d]	—	—
East Twin, Mich. Schneider 1973a	336	6.7	119[b]	18	13.5	3.4	54
Hoover, Ohio Momot et al. 1977	1,143	6.5	199	31	13.6	—	—
Wilson, Minn. Johnson 1977	245	6.6	51[b]	8	15.5 23.4(>200 mm)	—	—
Erickson, Wis. Helm 1958	44	3	65[b]	22	18.7[d]	—	—
West Okoboji, Iowa Rose 1957	1,540	12.0	261[b]	22	24.6[d]	—	—
Oneida, NY Forney 1967	20,640	6.8	165	24	25.0	—	—
Little John, Wis. Helm 1958	62	4	94	24	28.0[d]	—	—
Spauldings, Wis. Threinen and Helm 1952	11	2.5	102[b]	41	33.6	—	—
Storm, Iowa Rose 1950	1,238	2.0	185[b]	93	37.0	2	305

[a] All that were estimated; usually other species were present but not included.

[b] Converted from total alkalinity measures by the formula of Ryder (1964): TDS (total dissolved solids) = 1.1913 (total alkalinity) + 23.5 ppm. The alkalinity values for some Iowa lakes came from Bachmann (1967).

[c] Treated with rotenone. All other estimates were by mark-and-recapture techniques, usually for walleyes over 300 or 350 mm.

[d] Numbers converted to weights on the assumption that mean weight was 0.68 kg (1.5 lb) except that in Little John Lake a mean weight of 0.45 kg was used since this was judged to be a better average by Helm (correspondence).

TABLE 2. Biomass (kg/ha) of yellow perch and all fish in 18 lakes where they were less than 20% of the fish biomass.

Citation and lake	Area (ha)	Mean depth (m)	Alkalinity (ppm)	Biomass Perch	Biomass Total	Method[a]
Nova Scotia, Smith 1940						
Trefry's	22	—	—	1	19	p
Tedford	21	2.5	—	2	40	p
Minn., Hooper 1951						
Demming	5	3.5	25	2	22	p
Indiana, Ricker 1942						
Shoe	17	4	—	2	180	m
Mass., Stroud 1953						
Ponkapoog Pond	—	—	—	4	48	p
Iowa, Rose 1950						
Storm	1238	2	136	7	305	m
Wis., O'Donnell 1953						
West Twin	5	6	—	9	103	p
Mich. Schneider 1973a						
O'Brien	4	4.5[b]	167	2	50	p
Deep	6	9[b]	—	2	71	p
Howe	5	3.5[b]	51	2	71	p
Scaup	2.4	2	121	3	50	m
Walsh	4	3[b]	138	3	171	p
Cub	11.3	3.3	10	11	70	m
Kimes	2.8	2.7	—	12	256	p
Mill	55	1.6	140	16	130	m
Pond 4	0.6	—	—	20	127	p
Cassidy	19	1	127	27	162	m
Wintergreen	16	—	—	36	404	m

[a] p = estimate by chemical treatment; m = mark-and-recapture estimate.

[b] Mean depth not available, estimates at 0.5 maximum depth.

ment. However, production estimates involve data on standing crop by size or age-groups, individual growth rates, and mortality rates. Therefore, very little annual production information (Table 5) is available on walleye or perch populations. Because sustained harvest cannot exceed annual production, walleye yields from these lakes should not exceeds 1–3 kg/ha.

Yield

Annual yield statistics are the most readily available indicators of fish production. If yields only from lakes subjected to moderately intensive or intensive fishing are used and if the fishery is maintained several years, the yield statistics probably are representative of production (Ryder et al. 1974).

Perch yield data were not analyzed. Few perch populations are subject to consistently intensive fishing because the perch fishery is secondary to that for other species. The data that I analyzed cover a wider range of lake types than those reported by Adams and Olver (1977), but the yields were recorded in a less standardized manner and did not always cover enough years to indicate sustained yields. My search was not exhaustive, and yield data are scattered, often in reports with limited distribution or in unpublished files.

The annual commercial yields of walleye (Table 6) ranged from 0.04 to 3.06 kg/ha. Hebden and Contact lakes had larger yields of lake trout than of walleye and perhaps should not be included as percid lakes. Lakes Michigan and Ontario had their largest yields of walleye only after lake trout had been largely eliminated. Perhaps only Lake of the Woods, Lake St. Claire, Red Lake, and Lake Erie, lakes with yields of 1.35–3.06 kg/ha, are representative of percid populations. With these four lakes there is no correlation between yield of walleye and area, mean depth, total dissolved solids, or MEI.

The average yield (Y) decreases with latitude in degrees north (L) if Lakes Michigan, Huron, Ontario, Hebden, and Contact are left out:

TABLE 3. Biomass (kg/ha) of yellow perch and all fish in lakes where they were at least 20% of the fish biomass.

Citation and lake	Area (ha)	Mean depth (m)	Alkalinity (ppm)	Biomass		Method[a]
				Perch	Total	
Nova Scotia, Smith 1961						
Boar's Back	22.6	2.5	—	4.5	19	p
New Brunswick, Smith 1939						
Jessie	18.2	2.4	10	5.2	23	p
Ont., Chadwick 1976						
Red Deer	6.2	3.7	26	10	15	p
Mass., Stroud 1953						
Wineconnet	—	—	—	17	62	p
N.Y., Vashro 1975						
Oneida	20,640	6.8	90	35	—	m
Wis., O'Donnell 1943						
Long	11	3	—	39	155	p
Minn., Peterson 1955						
Camp 4[c]	6.7	4.5	—	40	71	p
Mich., Schneider 1973a						
Fitzek	2.5	—	—	9	36	p
Twin	8.7	13.7[b]	5	11	19	p
Linnbeck	2.1	3.8[b]	190	12	54	p
Booth	6.5	4.7[b]	125	17	40	p
East Twin	33.6	2.0	—	22	54	m
Airport	2.8	4.2[b]	5	26	27	p
Pike #4	1.9	2.7	153	27	82	p
East Fish	5.5	6.5[b]	196	35	56	p
Swanzy	8.2	7[b]	20	46	58	p
Grebe	29	2	75	48	131	m
Marsh	27	5	6	53	59	m
Ford	4.7	5[b]	127	65	96	p
Mean				27	59	

[a] p = estimate by chemical treatment; m = mark and recapture estimate. In Lake Wineconnet only one cove was rotenoned.

[b] Mean depth not available; estimated at 0.5 maximum depth.

[c] The estimate, given as 64 kg/ha of littoral area, was corrected to the area of the entire lake to be comparable with data from the other lakes.

$$Y = 6.36 - 0.096\,L;\ r = -0.58,\ P < 0.05$$

Yield also increases with total dissolved solids (T):

$$Y = 0.29 + 0.008\,T;\ r = 0.61,\ P < 0.05$$

However yield also shows a trend to increase with mean depth ($r = 0.32$, $P > 0.05$) which is the reverse of the expected relationship and therefore for this series of lakes, MEI is not as good a predictor of yield as is the total dissolved solids.

The yield also increases with the area (A) of the lakes in this series:

$$Y = 1.17 + 0.0007\,A;\ r = 0.58,\ P < 0.05$$

Rounsefell (1946) found the yield to decrease with increasing area of lakes. The fact that the eight lakes under 86,000 ha were all in Saskatchewan probably influenced the positive correlation in the data.

Multiple regression analysis indicated that the following would account for 55% for the variation in yield compared with 37% accounted for by total dissolved solids:

$$Y = 0.359 + 0.0063\,T + 0.00058\,A$$

Addition of latitude, mean depth, and MEI did not materially improve the regression.

The annual yield to sport fishing averaged 3.7 kg/ha (Table 7) which was greater than the average commercial yield. Many of these data are for a single year of fishing rather than averages over several years, but the available averages

TABLE 4. Biomass (kg/ha) in lakes with only yellow perch.

Citation and lake	Area (ha)	Mean depth (m)	Alkalinity (ppm)	Biomass	Method[a]
Mich., Schneider 1973a					
Cassidy	19	1	127	39	m
Section 4 pond	1.3	11+	149	53	p
South Twin	1.7	0.7	106	65	p
Jewett	5	2	33	70	m
Mass., Mullan and Tompkins 1959					
Round Pond	1.4	—	—	56	p
N.Y., Regier 1962					
Vann Pond	0.2	—	—	63	2 y
Mich., Schneider 1973b					
Cattail ponds	—	—	—	94	
Plankton ponds	—	—	—	121	
Ill., Buck and Thoits 1970					
Iota Pond	0.4	—	149	106	1 y
				112	2 y
Alpha Pond	0.4	—	203	161	1 y
				215	2 y
Theta Pond	0.4	—	117	206	3 y

[a] p = estimate by chemical treatment; m = mark and recapture estimate; y = population when drained after 1, 2, or 3 yr growth.

TABLE 5. Annual production ($kg \cdot ha^{-1} \cdot yr^{-1}$) of walleye and of yellow perch.

Lake and citation	Ages included	Production		
		Mean	Range	Years
	Walleyes			
West Blue, Man.				
Kelso and Ward 1977	I–VI	2.1	—	1969
Dexter, Ont.	IV+	4.1	—	—
Moenig 1975	IV+[a]	7.8	—	
Clear, Iowa	III+	1.21	0.42–3.07	1948–73
Carlander and Payne 1977	I+	3.08	0.91–6.98	1947–73
Hoover Reservoir, Ohio	II+	2.16	1.31–4.05	1967–73
Momot et al. 1977				
	Perch			
Red Deer, Ont.		21.9	—	1974
Chadwick 1976				

[a] Including reproductive products.

are similar to those from single years. Additional data on mean depths and on water chemistry and other factors may be available, but there is no indication that these would provide significant correlations.

There is, however, a significant correlation between yields and latitude, $r = -0.395$, $P < 0.02$, and between yields and area of the lake, $r = -0.366$, $P < 0.03$. Multiple regression analysis gave

$$Y = 18.52 - 0.3197\,L - 0.00002\,A$$

The combined regression, $r = 0.476$, accounts for 22.6% of the variance, whereas simple regression on latitude accounted for 15.6%. Increased yields to the south are to be expected because the growing seasons are longer, and yield is a function of production more than of biomass. Data on growth

TABLE 6. Annual yield (kg/ha) of walleye and all fish to commercial fishing

Citation and lake	Area (1000 ha)	Lat. (°N)	Mean depth (m)	TDS (ppm)	MEI	Yield Walleye	Yield All species	Years
Baldwin and Saalfeld 1962[a]								
Michigan	5802	44	84	118	1.4	0.04	1.95	1951–60
Ontario	1948	44	80	155	1.9	0.06	0.5	1951–60
Huron	5960	45	59	195	3.3	0.17	1.6	1891–1900
Sask., Rawson 1957a								
Churchill[b]	43	56	9	136	15	0.4	2.7	1941–55
Ille a la Crosse	45	55	8	185	23	0.5	3.2	1951–55
Frobisher	31	56	6	79	13	0.7	2.35	1966–55
Little Peter Pond	19	56	5	44	29	1.2	6.9	1941–55
Big Peter Pond	55	56	14	137	10	1.6	6.2	1941–55
Sask., Rawson 1957b								
La Range	124	55	13	149	11	0.2	1.1	1946–50
Sask., Koshinsky 1965								
Hebden	0.47	55	8	45	6	0.04	1.23	1956–64
Contact	1.42	55	7	55	8	0.11	2.1	1956–64
Little Deer	0.36	55	6	55	9	0.44	2.8	1956–64
Sulphide	0.43	55	4	55	14	0.71	4.25	1956–64
Sask., Atton and Kallemeyn unpublished data								
Peter Pond	74	56	11	140	12	1.7	9.2	1956–72
Churchill	43	56	9	128	13	2.2	12.6	1956–72
Ont., Chevalier 1977								
Rainy	86	48	10	57	6	1.0	4.4	1924–74
Minn., Heyerdahl and Smith 1972								
Lake of the Woods	357	49	8	83	10	1.35	4.88	1930–70
Minn., Heyerdahl and Smith 1971								
Red	117	48	6	275	32	2.71	4.57	1930–69
Minn., Smith 1977								
Red[b]	117	48	6	275	32	2.1	4.09	1954–75
						2.65	4.19	1930–53
Baldwin and Saalfeld 1962								
St. Claire	119	42	3	208	69	1.75	5.92	1891–1900
Erie	2572	42	18	196	11	3.06	7.25	1931–60

[a] Yields for the decades with the highest average walleye catch. Bluepike and/or sauger were included with walleye in Ontario, Huron, Erie, and St. Clare data.

[b] Not used in further calculations.

of walleye tabulated by Carlander (1953) and Colby et al. (1977) indicate that growth rates increase from the north to the south. The negative correlation between yield and area of the lake may be related to decreased fishing effort per hectare as distance from shore increases.

Data from the Minnesota Department of Natural Resources indicated sport fishing yields of walleye from 15 lakes classified by W. J. Scidmore (personal communication) as warmwater rather than percid lakes averaged 2.4 $kg \cdot ha^{-1} \cdot yr^{-1}$ and ranged from 0.04 to 7.25. The yield from one other lake was considered as exceptional, 21.3 kg/ha, and not included in the mean. Walleye may be quite abundant even where other predators are more abundant.

Conclusion

The available data point to our lack of information and suggest merely the probable magnitude of walleye and perch production. The lack of correlation between biomass or yields and the usual indicators of productivity probably is largely because walleye or perch populations do not bear a constant relationship to the total fish biomass or yield. The morphoedaphic index may indicate the potential yield from a body of water, but the proportion of the yield varies according to the

TABLE 7. Annual yield (kg/ha) of walleye, other predators, and all fish to sportfishing in 48 percid lakes arranged in order of increasing yield

Lake and citation	Area (ha)	Lat. (°N)	Mean depth (m)	TDS (ppm)	MEI	Yield			Yrs covered
						Walleye	Other predators	Total	
LaRonge, Sask. Rawson 1957b	123,616	52	13	149	11	0.15	—	—	6
St. Clair, Ont. Johnston 1977	119,139	42	3	208	69	0.19	—	—	6
Seagull, Minn. Micklus 1959	1,512	46	—	—	—	0.5	—	—	1
Eagle, Ont. Chevalier 1975	27,692	48	3	—	—	0.8	0.9	—	1
Lake of the Woods, Minn. Scidmore[a]	122,316	49	7	83	12	1.0	0.2	—	3
Cutfoot Sioux, Minn. Moyle and Franklin 1953	953	47	—	—	—	1.0	5.9	—	1
Nipissing, Ont. Anthony and Jorgensen 1977	85,500	46	4.6	80	11	1.0	1.2	2.9	1
Lost Island, Iowa Moen 1960a	510	43	2.5	290[b]	116	1.1	—	285	1
Pike, Minn. Scidmore[a]	328	47	7	99	14	1.2	—	1.3	2
Kegonsa, Wis. Frey et al. 1939	1,273	42	—	—	—	1.3	—	10.7	1
Green, Minn. Moyle and Franklin 1953	2,244	45	—	—	—	1.3	3.8	—	1
Waubesa, Wis. Frey et al. 1939	823	43	—	—	—	1.5	—	2.0	1
Winnibigoshish, Minn. Schneider 1977	28,256	46	4.6	169	45	1.7	—	5.0	2
Clear, Iowa Moen 1959, 1960a	1,474	43	3.6	230	64	1.8	—	16.8	2
Edward, Minn. Scidmore[a]	822	45	11	—	—	2.0	—	—	3
Cass, Minn. Scidmore[a]	6,313	47	7.6	180	24	2.1	—	6.2	5
Leech, Minn. Scidmore[a]	45,123	47	5.1	172	34	2.1	—	4.8	3
Splithand, Minn. Scidmore[a]	575	47	5.5	137	25	2.4	—	5.6	3
Toad, Minn. Scidmore[a]	679	46	6.4	183	29	3.0	—	10.9	2
Lac des Mille Lacs, Ont. Elsey and Thomson 1977	24,114	48	6.8	68	10	3.1	1.3	5.2	4
Moose, Minn. Scidmore[a]	485	46	7.9	163	21	3.2	—	4.6	5
Many Point, Minn. Scidmore[a]	694	47	9.1	168	18	3.3	—	8.5	3
Andrusia, Minn. Scidmore[a]	611	46	7.9	177	22	3.3	—	9.5	5

TABLE 7. (*Concluded*)

Lake and citation	Area (ha)	Lat. (°N)	Mean depth (m)	TDS (ppm)	MEI	Yield			Yrs covered
						Walleye	Other predators	Total	
Norris, Tenn. 1974 Fitz and Holbrook Unpublished data	13,840	36	18	127	7	3.5	—	—	1
Ingham, Iowa Moen 1959	170	43	25	163[b]	65	3.6	5.6	—	1
Detroit, Minn. Moyle and Franklin 1953	1,223	47	—	—	—	3.7	5.1	—	1
Mille Lacs, Minn. Scidmore[a]	53,420	46	6.2	133	21	4.0	—	6.0	2
Wolf, Minn. Scidmore[a]	425	47	8.5	167	20	4.8	—	15.2	5
Wilson, Minn. Johnson 1977	245	47	6.6	51	8	4.9	0.5	—	3
Little Pine, Minn. Scidmore[a]	824	46	8.5	222	26	6.1	—	11.6	3
West Okoboji, Iowa Moen 1960b	1,594	43	12	261[b]	22	6.2	—	62	3
Oneida, N.Y. Grosslein 1961	20,640	43	6.8	90	13	6.5	—	—	3
Black Hawk, Iowa Moen 1960a	387	42	2	260[b]	103	6.7	—	117	1
Big Bearskin, Wis. Bersing 1940	229	44	—	—	—	7.3	—	—	1
Spirit, Iowa Moen 1960a	2,168	43	5.2	271[b]	52	7.7	—	26.5	4
East Okoboji, Iowa Moen 1960b	567	43	2.8	272[b]	97	8.0	—	77	3
Escanada, Wis. Kempinger and Carline 1977	119	45	4.3	43	10	9.0	—	19.8	27
Norris, Tenn. 1963 Fitz and Holbrook Unpublished data	13,840	36	18	127	7	10.8	—	—	1
Escanaba, Wis. Churchill 1957	119	45	4.3	43	10	12.9	—	21	8

[a] Data from files and reports of Minnesota Department of Natural Resources by W. J. Scidmore, 1976.
[b] Calculated from total alkalinity by the formula from Ryder et al. (1974).

species composition of the population and catch. In many of the lakes covered in this report there is evidence of overfishing for walleye, and in few cases was the yield sustained over a sufficient number of years for the average yields to be valid measures of annual production.

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Yield Properties and Structure of Boreal Percid Communities in Ontario[1]

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ADAMS, G. F., AND C. H. OLVER. 1977. Yield properties and structure of boreal percid communities in Ontario. J. Fish. Res. Board Can. 34: 1613–1625.

A synoptic review of yield data for 70 northern Ontario lakes from 1917 to 1973 showed that percids, mainly walleye (*Stizostedion vitreum vitreum*) constituted about one-third, by weight, of the total fish yield. This relationship, which was independent of fishing effort, lake size, and lake productivity, is considered to be an emergent property of this type of fish community and represents a degree of homeostasis within the community under exploitation. The relation of percid yield to theoretical yield (based on the morphoedaphic index — MEI) reflected organizational structure and suggested the existence of a community (percid) component within the MEI, and from this we recommend upper limits of percid harvest for boreal percid lakes.

Most (83%) of the 70 lakes had an average total yield of less than 2.5 $kg \cdot ha^{-1} \cdot yr^{-1}$, 53% (37 lakes) yielding less than one-half of the theoretical yield (average 3.4 $kg \cdot ha^{-1} \cdot yr^{-1}$). Long-term average yields exceeded the theoretical maximums in only 11 lakes. Mesotrophic to slightly eutrophic waters appeared as optimum for percid yields.

Inferences from the data suggest an unexploited boreal percid community is characterized by high community stability and low net community production with resiliency low because of the low productive capacity of the waters. A yield index (RYI), which was assumed to reflect both effort and vulnerability to exploitation, showed that fishing intensity tended to be higher on the smaller, less productive lakes in this study.

Key words: Percidae, *Stizostedion*, community ecology, yield properties, management implications

ADAMS, G. F., AND C. H. OLVER. 1977. Yield properties and structure of boreal percid communities in Ontario. J. Fish. Res. Board Can. 34: 1613–1625.

Une revue synoptique des rendements de 70 lacs du nord de l'Ontario entre 1917 et 1973 démontre que les percidés, principalement le doré jaune (*Stizostedion vitreum vitreum*) constituent environ un tiers, en poids, du rendement total en poisson. Indépendante de l'effort de pêche, de la grandeur et de la productivité du lac, cette relation est considérée comme propriété émergente de ce type de communautés de poissons et représente un degré d'homéostasie à l'intérieur de la communauté sous exploitation. La relation entre le rendement en percidés et le rendement théorique (fondé sur l'indice morphoédaphique (IME)) reflète une structure organisationnelle et suggère l'existence d'une composante de la communauté (percidés) dans l'IME. Partant de ceci, nous recommandons des limites supérieures de récolte de percidés pour les lacs boréaux à percidés.

La plupart (83%) des 70 lacs ont un rendement total moyen inférieur à 2.5 $kg \cdot ha^{-1} \cdot a^{-1}$, 53% (37 lacs) ayant un rendement inférieur à la moitié du rendement théorique (moyenne 3.4 $kg \cdot ha^{-1} \cdot a^{-1}$). Les rendements moyens à long terme dépassent les maximums théoriques dans seulement 11 lacs. Des eaux allant de mésotrophes à légèrement eutrophes semblent être optimales pour les rendements en percidés.

On déduit des données qu'une communauté de percidés boréale est caractérisée par une haute stabilité et une faible production nette, avec faible résistance à cause du peu de capacité de production des eaux. Un indice de rendement (RYI) considéré comme reflétant à la fois l'effort et la vulnérabilité à l'exploitation, démontre que l'intensité de pêche tend à être plus forte dans les lacs plus petits et moins productifs couverts dans cette étude.

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THE purpose of this paper is to review long-term catch data in 70 commercially fished lakes in northern Ontario, to identify yield properties and draw general inferences from this information to improve our operational understanding of percid communities.

From the more than 500 lakes[3] that have been commercially fished in this region, the 70 (Table 1) were selected on the basis of consistency of fishing effort, dependence on percid populations by the fishery and availability of selected morphometric and edaphic measurements for subsequent analyses. The intent was to sample lakes comprising a relatively homogeneous set of boreal percid communities subject to a wide range of harvesting stress.

These lakes, which are relatively unproductive, share a high degree of ecological similarity on the basis of their geographic setting, their fish fauna and man's influence upon them. Because of their geographic location, the limnological conditions and the fisheries have varied less over time than their more fertile southern counterparts. For this reason, it can be assumed that the present species complex of walleye (*Stizostedion vitreum vitreum*), lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*), and sucker (*Catostomus* spp.) is optimum for community persistency in these lakes. For the most part, these lakes continue to be important producers of highly preferred sport and commercial fish.

The monitoring of relative stock abundance over time provides confidence for theoretical yields (Henderson et al. 1973) and alternative management strategies. Yield relationships revealed in this study offer insights and guidelines for identifying waters for optimum percid yields, setting initial harvesting rates for percids, establishing upper limits to percid harvests in boreal lakes and selecting areas for experimental management. The inferences drawn from this set of Ontario lakes are fundamental organizational properties of percid communities which should apply to the management of a broad spectrum of lakes.

Regional Geography

The study lakes are in the region from 80°W to 95°W and from 48°N to 54°N, not including Lake Superior (Fig. 1). The entire area was overlain by the Laurentide ice sheet in the Wisconsin glaciation. As the ice retreated, large glacial lakes were created (Flint 1957). The lakes, which were modified to various degrees through erosion and deposition by glacial ice, are underlain by Precambrian rock of the Canadian Shield that consists mainly of sedimentary and volcanic beds with large magmatic intrusions (Anon. 1957).

The region is characterized by its profusion of water. The predominant feature of the landscape is a surface of low relief traversed by numerous lakes and streams that drain into major rivers. The drainages are meandering, characterized by rivers that broaden frequently into lakes. Precipitation is moderate and, because of the morphometry, high rates of flushing are atypical.

Two major drainage systems in the study area, the Hudson Bay drainage and the Atlantic drainage, were created during the glaciation period. The Hudson Bay drainage draws the water north and northeast, chiefly via the watersheds of the Nelson and Hayes rivers and the Severn, Winisk, Attawapiskat, Albany, and Moose rivers, respectively. The Precambrian peneplain slopes gently to the west and south of the height of land (Fig. 1), and is drained by the English and Winnipeg rivers (Nelson River watershed) of the Hudson Bay drainage and by the Nipigon River and other minor rivers of the Lake Superior watershed (Atlantic drainage).

Lying in the humid microthermal climate zones, the lakes are in a region that experiences, from north to south, 1500–3000 degree-days over 5.6°C (140–180 days) and an average time of 210–150 days of lake ice cover (Anon. 1974). The mean daily July temperatures range from 14 to 19.4°C (Anon. 1963). Average annual precipitation ranges from 500 to 760 mm, and the number of days of precipitation from 120 to 160 (160 to 185 days in the northeastern area). Average annual runoff is mainly from 20 to 30 cm. The period of maximum flow is primarily from April to June with most of the rivers running less than 10,000 cfs (only the Albany and Moose rivers exceed 40,000 cfs). The altitude does not exceed 600 m. The Albany River, which has one of the highest flushing rates, flows from Lake St. Joseph (altitude, 370 m) and collects water for 850 km.

The Commercial Fisheries

This region has supported commercial fisheries since the 1880s and the character of the harvest was substantially determined by opportunities for export to United States markets. In general, the fisheries expanded north toward relatively unexploited lakes as reliable transportation permitted.

Catch reports, excluding bait fisheries, identified 25 species with the majority unimportant in the harvest (Adams and Kolenosky 1974). Commercial fishing was, historically, directed at the dominant species — primarily walleye, lake whitefish, and northern pike. In the study lakes, these species comprised a major portion of the total catches.

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[3] Unpublished records maintained by the Ontario Ministry of Natural Resources, Toronto, Ont.

Catch data in this paper are based entirely on reports submitted by commercial fishermen. Although regulations required each commercial licensee to report all fish landed, there was evidence, in some operations, that discarded or unsold catches were not recorded. Occasionally, catch data for some species were not available or were inaccurate because fishermen grouped different species into specific market categories or pooled portions of their catches as unmarketable. The catch data disregard domestic consumption, an important factor in remote northern communities (Rogers 1972). The data, originally recorded in pounds (round weight), were converted to metric units.

All of the 70 lakes were commercially fished at least 10 yr within a span of 20 yr. Over a period of 50 yr (57 for Lake Nipigon) the set of lakes represented an average of 25.4 yr of exploitation per lake (total of 1778 yr). Except in those lakes near urban centers, particularly Lake of the Woods and Rainy Lake, exploitation appeared to be the only stress imposed on the fish populations in these lakes.

Few of the lakes were fished more than 120 days a year. Fishing exceeded 6 mo a year only in the larger lakes and in several that were readily accessible by road.

Effort statistics were not available in a form permitting computation of catch-per-unit-effort estimates. To compensate, a yield index (the ratio of total yield to theoretical yield, expressed as a percentage) was formulated. This yield index, called relative yield intensity (RYI), is assumed to reflect both effort and vulnerability to exploitation (see Table 1 for individual lake values).

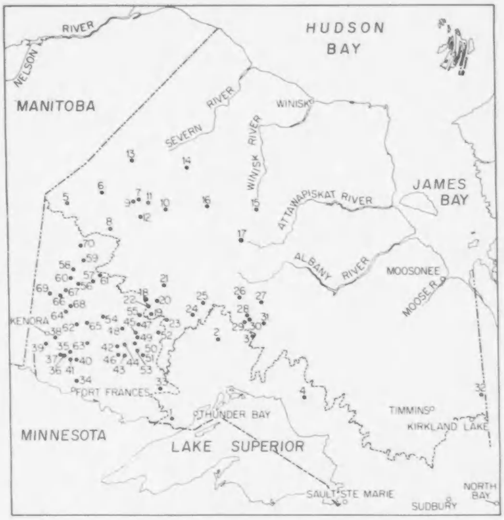

FIG. 1. Locations of the study lakes. For names, see Table 1. Stippled line indicates height of land.

Most of the 70 lakes have been regulated since the mid-1950s under a catch-quota system, primarily for whitefish and walleye. According to Adams (1972b), few fisheries reach their allowable harvest under this system. Yield was probably limited by effort in many lakes.

In 1970, with the discovery of unacceptable levels of mercury contamination in fish, a number of the fisheries were closed. Many remote fisheries ceased operations because the prime species (walleye) could not be marketed. The affected years for these lakes were omitted from the analyses. According to Adams (1972a), mercury contamination, as either a primary or a secondary factor, was the major cause of declines in harvests after 1970.

Selected Lake Characteristics

Though most of the study lakes are in chains of lakes in various river systems, they are treated here as limnologically discrete. Data on area, mean depth and total dissolved solids (TDS) were obtained, along with other physical, chemical, and biological measurements, through lake surveys conducted by the Ontario Ministry of Natural Resources (formerly the Ontario Department of Lands and Forests) from 1961 to 1974. All measurements were recorded in English units and converted to metric equivalents.

The total area of the 70 lakes (16,416 km^2) comprised approximately 20% of the total surface area of water in the region. The lakes ranged in size from 4,481 km^2 (Lake Nipigon, the largest lake entirely within Ontario) to just more than 11 km^2 (Table 1). The extent of this range can be appreciated when we consider that the three lakes that exceeded 1,000 km^2 and the 24 lakes that exceeded 100 km^2 represented 50 and 88% of the total surface area of the 70 lakes, respectively. The effect of lake surface area on a fishery and its yield has been discussed by Ryder et al. (1974).

The range of mean depths was equally broad (Table 1), as shown by the extreme range between Meta Lake (1.7 m) and Lake Nipigon (54.9 m), although most of the lakes had a mean depth less than 15 m.

Total dissolved solids (TDS) varied between

TABLE 1. Selected morphometric and edaphic features, morphoedaphic indexes (MEI), theoretical and total yields, percid yields, and relative yield intensities (RYI) for 70 commercially fished lakes in northern Ontario, 1924–73[a].

							Yield ($\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$)			
Lake	Lake number[b]	Surface area (ha)	Mean depth (m)	TDS	MEI[c]	Years fished	Theoretical ($\hat{Y}$)	Total (Y)	Percid (%)	RYI[d] (%)
Whitefish	1	3,015	1.8	62	34.4	27	6.7	1.5	1	22
Nipigon	2	448,060	54.9	80	1.5	57	1.6	1.0	13	59
Onaman	3	11,488	2.2	40	18.2	38	5.0	2.3	11	45
White	4	5,888	8.7	71	8.2	27	3.5	0.2	30	7
Deer	5	14,300	21.6	33	1.5	26	1.7	0.7	44	43
Sandy	6	49,730	5.5	113	20.5	15	5.3	0.2	52	4
Magiss	7	5,439	3.0	71	23.7	13	5.6	1.7	25	31
MacDowell	8	10,360	6.1	56	9.2	24	3.7	2.6	43	69
Nikip	9	5,517	1.8	75	41.7	12	7.2	1.1	26	15
North Caribou	10	31,326	5.5	152	27.6	18	6.1	1.1	21	18
Weagamow (Round)	11	12,430	6.7	67	10.0	22	3.9	2.0	28	51
Windigo	12	8,550	7.3	84	11.5	16	4.1	2.3	11	55
Sachigo	13	25,900	2.7	80	29.6	13	6.2	0.4	25	6
Big Trout	14	61,640	15.8	68	4.3	17	2.7	0.5	9	18
Winisk	15	26,160	3.4	83	24.4	20	5.8	0.3	55	6
Wunnummin	16	23,580	6.1	74	12.1	22	4.2	0.8	70	19
Attawapiskat	17	26,160	5.8	83	14.3	16	4.5	0.5	37	12
Churchill	18	4,179	5.2	26	5.0	15	2.8	0.9	59	32
Hooker	19	2,113	5.8	25	4.3	11	2.7	2.1	41	79
Miniss	20	6,314	6.0	25	4.2	13	2.6	1.1	48	42
St. Joseph	21	51,540	5.1	41	8.0	40	3.5	0.8	51	23
St. Raphael	22	4,027	4.8	25	5.2	10	2.9	0.9	61	32
Savant	23	12,041	7.9	22	2.8	35	2.2	0.7	31	33
Smoothrock	24	9,824	5.5	18	3.3	33	2.4	0.3	30	11
Whitewater	25	10,529	4.6	14	3.0	28	2.3	0.3	16	11
Kagianagami	26	8,990	4.6	74	16.1	28	4.8	0.8	48	16
Ogoki	27	6,616	2.6	71	27.3	21	6.1	0.8	31	14
Ara	28	4,930	4.4	36	8.2	27	3.5	1.5	22	42
Marshall	29	1,936	2.5	65	26.0	21	5.9	1.2	23	21
Meta	30	3,080	1.7	85	50.0	32	7.9	1.5	17	19
O'Sullivan	31	4,292	8.3	114	13.7	19	4.5	1.8	38	39
Abitibi[e]	32	79,770	3.5	62	17.7	48	5.0	0.4	38	8
Lac des Mille Lacs	33	24,112	6.8	23	3.4	30	2.4	0.9	66	37
Rainy[e]	34	70,149	9.3	55	5.9	50	3.1	4.2	25	137
Atikwa	35	5,388	13.2	23	1.7	15	1.8	1.7	32	94
Caviar	36	3,186	10.1	31	3.1	24	2.3	6.0	16	261
Dogpaw	37	1,994	10.4	47	4.5	27	2.7	12.5	17	463
Dogtooth	38	2,478	9.8	15	1.5	19	1.7	5.1	6	303
Lake of the Woods[e]	39	246,760	7.2	69	9.6	50	3.8	3.2	37	83
Lawrence	40	1,871	22.2	22	1.0	14	1.4	1.4	33	100
Rowan	41	4,146	1.8	48	26.7	21	5.9	2.0	24	34
Basket	42	4,267	6.0	21	3.5	35	2.4	2.2	30	91
Indian	43	3,963	9.4	24	2.5	37	2.1	2.5	24	121
Kukukus	44	4,129	5.0	26	5.2	23	2.9	1.3	53	44
Lake of Bays	45	4,662	12.2	31	2.5	43	2.1	1.2	38	56
Mameigwess	46	5,309	16.2	31	1.9	20	1.9	2.1	4	112
Marchington	47	3,640	8.0	25	3.1	12	2.3	1.6	32	68
Minnitaki West	48	18,087	17.8	44	2.5	30	2.1	1.0	23	48
Penassi	49	1,441	6.6	18	2.7	15	2.2	1.3	44	59
Press	50	3,764	5.6	22	3.9	35	2.5	1.2	49	47
Sowden	51	3,719	6.3	16	2.5	10	2.1	0.8	39	41
Sturgeon	52	16,239	21.3	28	1.3	47	1.6	2.1	21	131
Wintering	53	1,688	5.3	23	4.3	28	2.7	2.1	38	78
Lac Seul	54	129,500	7.6	93	12.2	47	4.2	1.6	35	38
Raggedwood	55	1,118	6.6	60	9.1	11	3.7	1.9	40	51

TABLE 1 (*Concluded*).

							Yield (kg·ha^{-1}·yr^{-1})			
Lake	Lake number[b]	Surface area (ha)	Mean depth (m)	TDS	MEI[c]	Years fished	Theoretical ($\hat{Y}$)	Total (Y)	Percid (%)	RyI[d] (%)
Gullrock	56	6,762	7.8	36	4.6	26	2.7	1.9	34	69
Little Trout	57	3,665	6.7	32	4.8	17	2.8	2.1	21	75
Little Vermilion	58	5,636	3.4	24	7.1	10	3.3	0.6	20	18
Nungesser	59	7,557	5.2	18	3.5	13	2.4	1.4	58	59
Red	60	17,676	14.6	29	2.0	42	1.9	1.2	17	65
Woman	61	2,035	10.3	37	3.6	35	2.4	2.9	18	121
Clay	62	3,088	7.9	58	7.3	32	3.4	2.8	24	83
Eagle	63	27,691	6.8	19	2.8	40	2.2	2.1	21	95
Ball	64	2,757	10.4	55	5.3	13	2.9	4.0	42	138
Cliff	65	2,263	10.6	74	7.0	13	3.3	1.7	5	51
Confusion	66	1,426	11.4	76	6.7	10	3.2	1.8	33	56
Longlegged	67	6,915	8.8	20	2.3	35	2.0	0.7	25	34
Oak	68	4,183	7.2	64	8.9	34	3.7	4.2	31	116
Sydney	69	5,827	19.8	16	0.8	31	1.3	2.7	32	215
Berens	70	2,790	4.7	23	4.9	20	2.8	0.9	54	31

[a]Lake Nipigon, 1917–73; [b]Number in Fig. 1; [c]TDS/mean depth; [d]$(Y/\hat{Y})$ 100; [e]Ontario portion of lake only.

14 and 152 ppm, although only eight lakes had a value greater than 80 ppm and 40 had less than 50 ppm (Table 1). If measured in late July or early August, a period approaching maximum nutrient stability, TDS is considered to represent the average annual edaphic condition for any watershed (Ryder 1964). Most lake surveys were conducted at this time. Although TDS may reflect the influence of other physiographic and morphometric features on the lake environment, this measurement and its relation to mean depth is used in this study only to calculate the morphoedaphic index, or MEI (Ryder 1965; Ryder et al. 1974), for the purpose of describing potential lake productivity and trophic status.

On the basis of MEI, the 70 lakes can be broadly placed into the oligotrophic-mesotrophic-eutrophic classification. According to Ryder (1965), an MEI of about 6.6 (metric) appears to separate oligotrophic from eutrophic lakes, with mesotrophic lakes showing an index near this figure. The MEI range for mesotrophic lakes is proposed to be narrow, not exceeding 1.4 units. As follows, most of the 70 lakes were either oligotrophic or eutrophic:

Trophic state	MEI range	No. of lakes	Mean yield (kg·ha^{-1}·yr^{-1})
Oligotrophic	0.8– 5.9	39	2.04
Mesotrophic	6.0– 7.3	4	1.72
Eutrophic	7.4–50.0	27	1.43

Sydney Lake (MEI = 0.8) represented extreme oligotrophy in the study lakes, and Meta Lake (MEI = 50.0) extreme eutrophy. Only Little Vermilion, Clay, Cliff, and Confusion lakes were classified as mesotrophic (Table 1).

Productivity in these lakes is low to moderate and they are less productive than most percid lakes (see this symposium). Potential or theoretical yield is that as defined by the MEI under the developmental constraints as outlined by Henderson et al. (1973). The highest theoretical yield was 7.9 kg·ha^{-1}·yr^{-1} and the average for all lakes was 3.4 kg·ha^{-1}·yr^{-1} (Table 2). Over one-half of the lakes had a theoretical yield of 2.0 to 3.9 kg·ha^{-1}·yr^{-1}. Only 2 lakes exceeded the optimum MEI of 40 (Ryder et al. 1974), both because of exceedingly low mean depths.

The underlying bedrock and soils and severity of the climate greatly limit the ability of the lakes to produce fish (Ryder 1972). While these extrinsic factors (nutrient availability, climate, etc.) are not the sole regulating or balancing forces in community dynamics, they are significant limiting factors to fish production in these lakes. Implicit in Ryder's (1965) model was the limitation of nutrients to primary production. A feature of most of the lakes which is redeeming of productivity is the extensive littoral zone, including irregular shorelines and a great number of islands.

Four levels of relative yield intensity (RYI) were selected and related to MEI:

RYI (percent)	No. of lakes	Morphoedaphic index (MEI)	
		Mean	Range
0– 29	19	19.8	3.0–50.0
30– 49	18	8.1	1.5–26.7
50–100	22	5.1	1.0–11.5
>100	11	3.6	0.8– 8.9

Generally, the highest RYI was found in the

TABLE 2. Frequency distribution of theoretical, total, and percid yield for 70 commercially fished lakes in northern Ontario, 1924–73.

	Number of lakes		
Range of yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Theoretical yield	Total yield	Percid yield
0– 0.09	0	0	8
0.1– 0.29	0	3	17
0.3– 0.49	0	5	14
0.5– 0.79	0	7	21
0.8– 0.99	0	8	4
1.0– 1.4	2	14	4
1.5– 1.9	7	12	1
2.0– 2.4	16	9	1
2.5– 2.9	13	5	0
3.0– 3.9	13	2	0
4.0– 4.9	6	2	0
5.0– 5.9	7	1	0
6.0– 6.9	4	1	0
7.0– 7.9	2	0	0
12.0–12.9	0	1	0
Average yield	3.4	1.8	0.5

more oligotrophic lakes. Ten of the eleven lakes which exceeded their theoretical yields (Table 1) were classed as oligotrophic.

Although the set of lakes was moderately homogeneous with respect to yield (a range of 0.2–12.5 $kg \cdot ha^{-1} \cdot yr^{-1}$, Table 1), the RYI indicates a range of fishing effort that may not be sufficiently uniform (Ryder et al. 1974) for application of the MEI. The lakes were subjected to multispecies fisheries that were continued long enough and were intense enough to activate some of the density-dependent, compensating factors (increased recruitment, changes in relative abundance, decreased natural mortality, increased growth rate) that tend to maintain the homeostasis of the lake system. By selecting four levels of RYI, the proportionality of long-term fish yields to MEI was made apparent (Fig. 2). Superimposing the four RYI curves on Ryder's (1965) yield curve for north-temperate lakes of North America may offer useful insights into identifying boreal percid lakes that are approaching upper limits of sustained yield.

The relationship between RYI and total yield, percid yield, lake area, and lake productivity (Table 3) suggested that vulnerability and its relation to effort was related to the size and productivity of the lake fished. Apparently effort and exploitation were concentrated on the smaller, less productive lakes, possibly because the fish populations in these lakes were more vulnerable to small fishing operations.

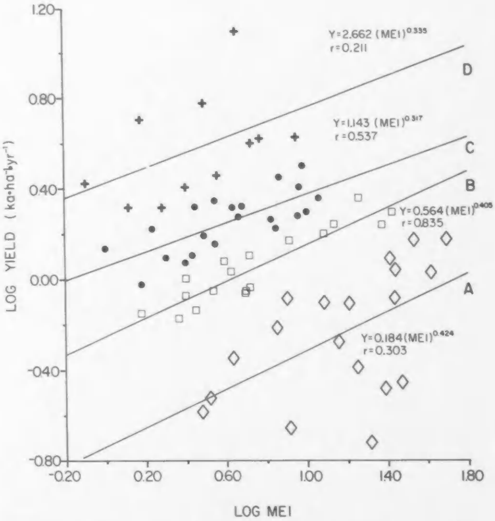

FIG. 2. Relations of average yield to lake productivity (MEI) for four levels of relative fishing intensity (RYI) for 70 commercially fished lakes in northern Ontario, 1924–73. A, RYI 0–29%; B, RYI 30–49%; C, RYI 50–100%; D, RYI >100%.

Yield Properties and Community Structure

As indicated by the catch composition for each of the 70 lakes (Table 4), the annual commercial yield was always dependent on a few species — those of highest market value. Coregonids (41.5%), percids (31.7%), and esocids (11.3%) comprised 84.5% of the total harvest. Percid yield was essentially walleye (99.7%). Market conditions and prices probably limited the harvest of northern pike. Although all lakes were fished for percids, they comprised, on the average, about one-third of the total catch. In almost three-quarters of the lakes, percids formed less than 40% of the harvest. Percids comprised more than 50% of the total catch in only 10 of the 70 lakes.

Long-term average total yields exceeded theoretical maximums in 11 lakes, whereas in 37 of the 70 lakes total yield was less than half the theoretical yield predicted by the MEI (Table 1). The majority of lakes (83%) had an average total yield of less than 2.5 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Table 1). The average yield of percids was 0.49 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Table 3) and exceeded 0.80 $kg \cdot ha^{-1} \cdot yr^{-1}$ in only 10 lakes.

In moderately to intensively fished lakes (RYI of 50–100%), percid yield averaged about 20% of the theoretical yield (Table 3). The yield of percids in relation to total yield varied little for

TABLE 3. Theoretical, total, and percid yields and lake areas (averages) in relation to five levels of relative yield intensity (RYI) for 70 commercially fished lakes in northern Ontario, 1924–73.

RYI (%)	Number of lakes	Average area (ha)	Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$) Theoretical ($\hat{Y}$)	Total (Y)	Percid[a] (Y_p)	Percid yield (%) ($Y_p/\hat{Y}$)	(Y_p/Y)
0– 29	19	22,991	4.92	0.70	0.20	4.1	28.6
30– 49	18	14,676	3.21	1.22	0.44	13.7	36.1
50–100	22	6,383[b]	2.74	1.89	0.57	20.8	30.2
>100	11	4,797[c]	2.34	4.39	0.91	38.9	20.7
All lakes			3.39	1.79	0.49	14.4	27.4
Intensity ≤ 100							31.5

[a] Total for walleye, sauger, and yellow perch (see Table 4).

[b] Excluding Lake Nipigon (448,060 ha) and Lake of the Woods (246,760 ha).

[c] Excluding Rainy Lake (70,149 ha).

those lakes in which the theoretical yield was not exceeded (RYI ≤100%), ranging between 28.6 and 36.1% and averaging 31.5%, or about one-third of the total yield. Further, the ratio of percid yield to total yield was independent of RYI, lake area and lake productivity. The latter relationship suggests a relatively homeostatic percid community under exploitation. Both relationships offer promise for experimental quota management.

Overfishing was suspected to have occurred in the 11 lakes for which total yield (averaged) exceeded theoretical yield as defined by the MEI. According to studies reported by Johnston (1915), Zoltai (1961, 1967), and Elson (1967), nine of these lakes (Rainy, Caviar, Dogpaw, Dogtooth, Ball, Oak, Sydney, Sturgeon, and Woman) are in the area once submerged by glacial Lake Agassiz. Lakes Indian and Mameigwess are shown to be in an area once modified by lake action (outwash deposits). Although lacustrine deposits suggest that theoretical yields are biased downward, measurements of high colloidal turbidity, a condition in this region of former submergence, are known to be a factor that can result in over-estimates of both TDS measurements and conductivity readings (R. A. Ryder personal communication). Consequently, it would be appropriate to reevaluate estimates of theoretical yield for these lakes.

Because five of the 11 lakes with RYI greater than 100 did not have high percid yields, they are not discussed further. The remaining six lakes (Sydney, Caviar, Rainy, Oak, Ball, Dogpaw) are all in the basin of extinct Lake Agassiz and each had a long-term percid yield greater than 0.85 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Table 4). The only other lakes that had long-term percid yields in excess of 0.85 $kg \cdot ha^{-1} \cdot yr^{-1}$ were MacDowell Lake and Lake of the Woods, although their long-term total yields were less than the theoretical yields. Annual yields of percids in these eight lakes tended to be erratic (Fig. 3).

Although an annual percid yield as high as 3.01 kg/ha was recorded for *Sydney Lake*, this occurred after a 7-yr period of nonfishing. Percid yields greater than 1.00 kg/ha were recorded for only 9 of the 31 yr of fishing on the lake and only twice from 1953 to 1973. Yield of percids increased gradually to 1.20 $kg \cdot ha^{-1} \cdot yr^{-1}$ (cumulative average) in 1948 and then declined to 0.86 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1973.

Caviar Lake showed a trend similar to that in Sydney Lake: a substantial increase in percid yield (cumulative average) throughout the early and middle years of the fishery to 1.14 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1963 and 1964 and a gradual decline to 0.97 $kg \cdot ha^{-1} \cdot yr^{-1}$ by 1971. The long-term average total yield in both of these lakes was 2–2½ times the theoretical yield.

In contrast to Sydney and Caviar lakes, *MacDowell Lake* (range of 0.08–3.03 $kg \cdot ha^{-1} \cdot yr^{-1}$) showed a pronounced upward trend in percid yield, particularly from 1969 to 1973 (Fig. 3). This may suggest the occurrence of a fishing-up process during these years. From 1963 to 1973, annual percid yields averaged 1.71 kg/ha, which is more than 3 times the average for the first 13 yr of fishing.

For *Rainy Lake*, average yields of percids (Ontario portion only) declined steadily from 1924: 1.76 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1924 to 1.06 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1973. This decline was most rapid from 1962, as during 1962 to 1973 the annual percid yields did not exceed 1.00 kg/ha and averaged 0.44 $kg \cdot ha^{-1} \cdot yr^{-1}$. Chevalier (1977)

TABLE 4. Average annual commercial catches (kg/ha) of various fish species (and groups of species) for 70 lakes in northern Ontario, 1924–73^a. (*catches < 0.01 kg/ha.)

Lake	Lake sturgeon	Lake trout	Lake whitefish	Other coregonids	Northern pike	Sucker	Burbot	Cen-trarchids	Other species	Not identified	Walleye	Sauger	Yellow perch	Total
Whitefish		0.01	1.41		0.02					0.03	0.02			1.49
Nipigon	0.01	0.13	0.63	0.04	0.01	*	*	*		0.01	0.11	*	*	0.95
Onaman			1.63		0.31	0.08				0.02	0.24		*	2.28
White			0.08	*	0.02	0.01	*			0.03	0.07	*		0.22
Deer		0.06	0.27	*	0.05	*	*			0.01	0.32			0.71
Sandy	*		0.04	*	*	*	*		0.05		0.10			0.19
Magiss	0.01		1.20		0.08						0.45			1.74
MacDowell			1.02	0.02	0.26	0.04				0.13	1.08			2.55
Nikip	0.02		0.70		0.07						0.28			1.07
North Caribou		0.01	0.79	*	0.07	*	*				0.23			1.10
Weagamow (Round)			1.40		0.03						0.55			1.98
Windigo	0.01		1.95		0.06						0.25			2.27
Sachigo	*		0.20		0.06						0.09			0.35
Big Trout		0.37	0.03		*						0.04			0.45
Winisk	0.02		0.12		*	*	*				0.18			0.33
Wunnummin	0.01		0.20		0.01	*				0.01	0.55			0.79
Attawapiskat	0.02		0.31		*						0.20			0.53
Churchill			0.19	0.02	0.09	0.04	0.02				0.52			0.88
Hooker		0.03	1.14	*	0.06						0.85			2.08
Miniss	*	0.01	0.35	0.02	0.11	0.03				0.03	0.52			1.08
St. Joseph	0.01	*	0.29	0.01	0.07	0.01	*			*	0.42			0.82
St. Raphael			0.30		0.06	*					0.56			0.92
Savant		0.06	0.32		0.09	0.02	0.01			0.01	0.22			0.73
Smoothrock	0.07	0.01	0.08	0.01	0.03	0.01				*	0.09			0.30
Whitewater	0.19	*	0.02	*	*						0.04			0.26
Kagianagami		0.03	0.30		0.07	0.01		*			0.37			0.78
Ogoki	0.29		0.17		0.12						0.25			0.83
Ara			0.89	*	0.24	0.02	*			0.01	0.32		*	1.48
Marshall			0.88		0.08						0.28		*	1.24
Meta			1.09		0.13	0.03					0.25		*	1.51
O'Sullivan		0.07	0.53		0.48					*	0.67			1.75

TABLE 4 (*Concluded*).

Lake	Lake sturgeon	Lake trout	Lake whitefish	Other coregonids	Northern pike	Sucker	Burbot	Cen-trarchids	Other species	Not identified	Walleye	Sauger	Yellow perch	Total
Abitibi	*		0.04	0.01	0.10	0.03		*	*	0.07	0.15	*	*	0.41
Lac des Mille Lacs			0.14	*	0.13	0.02	*			*	0.58		*	0.88
Rainy	0.01	*	0.38	0.55	0.94	0.61	0.22	0.03	*	0.39	1.03	*	0.03	4.19
Atikwa		0.15	0.65		0.11	0.11	0.10			*	0.54			1.67
Caviar		0.41	3.58	0.03	0.73	0.07	*	0.23		*	0.97	*		6.03
Dogpaw		0.68	6.96	0.04	1.44	0.10	0.01	0.99	*	0.07	2.16	*		12.45
Dogtooth		0.01	3.22	0.01	0.25	1.01	0.24	*			0.33			5.07
Lake of the Woods	*	0.02	0.34	0.18	0.68	0.26	0.17	0.02	0.07	0.22	1.14	0.03	0.02	3.15
Lawrence		0.19	0.28						0.44	0.01	0.45			1.37
Rowan		0.27	1.13		0.06	0.02	0.01				0.48			1.97
Basket		0.01	0.71	*	0.42	0.19	0.02			0.19	0.66		*	2.21
Indian		0.03	0.98	0.02	0.30	0.41	0.12			0.06	0.62			2.54
Kukukus			0.12		0.28	0.15				0.05	0.67			1.27
Lake of Bays		0.09	0.24		0.33	0.05				0.02	0.45			1.18
Mameigwess		0.21	1.54		0.05	0.11	*			0.07	0.09			2.08
Marchington			0.33	0.43	0.30						0.50			1.56
Minnitaki West		0.02	0.42	0.01	0.21	0.07	0.02			0.03	0.23			1.01
Penassi		0.05	0.28		0.29	0.05				0.04	0.56			1.27
Press			0.18	0.14	0.18	0.09	0.01			*	0.59	*		1.20
Sowden			0.12	0.02	0.15	0.11	0.07		0.02	0.03	0.33		*	0.85
Sturgeon		0.31	0.75	*	0.15	0.24	0.13		0.01	0.04	0.44			2.08
Wintering			0.12	0.03	0.71	0.42				*	0.78			2.07
Lac Seul		*	0.44	0.09	0.39	0.06	0.04			0.02	0.56			1.60
Raggedwood		0.04	0.99	0.03	0.05	0.02					0.76			1.89
Gullrock	*	*	0.76	*	0.14	0.17	0.16			0.01	0.63	*	*	1.88
Little Trout			1.34		0.25	0.02	*			0.04	0.44			2.09
Little Vermilion			0.14	0.04	0.16	0.01	*			0.14	0.12			0.61
Nungesser			0.27	0.04	0.15	0.07	0.04			0.02	0.83		*	1.43
Red		0.03	0.68	*	0.07	0.09	0.15			*	0.21	*		1.24
Woman		0.09	0.72	0.26	0.17	0.37	0.48			0.24	0.53		*	2.87
Clay			0.52	0.58	0.50	0.07	0.04	*	0.19	0.23	0.67			2.80
Eagle		0.03	0.69	0.29	0.30	0.13	0.09		*	0.12	0.41	0.01	*	2.08
Ball		0.01	1.11	0.22	0.83					0.14	1.68			3.99
Cliff	0.02	0.13	1.27		0.16	0.01	*				0.09			1.68
Confusion	*	0.11	0.75	*	0.10	0.22	0.04			*	0.60	*		1.83
Longlegged		0.02	0.32	0.01	0.07	0.05	0.01			0.01	0.18			0.67
Oak			0.57	0.52	0.92	0.56	0.07	*	0.18	0.11	1.31	0.01	*	4.25
Sydney		0.34	0.90	0.03	0.32	0.08	0.01			0.13	0.86			2.67
Berens	0.08		0.08	0.01	0.08	0.02				0.13	0.47			0.87

[a] Lake Nipigon, 1917–73.

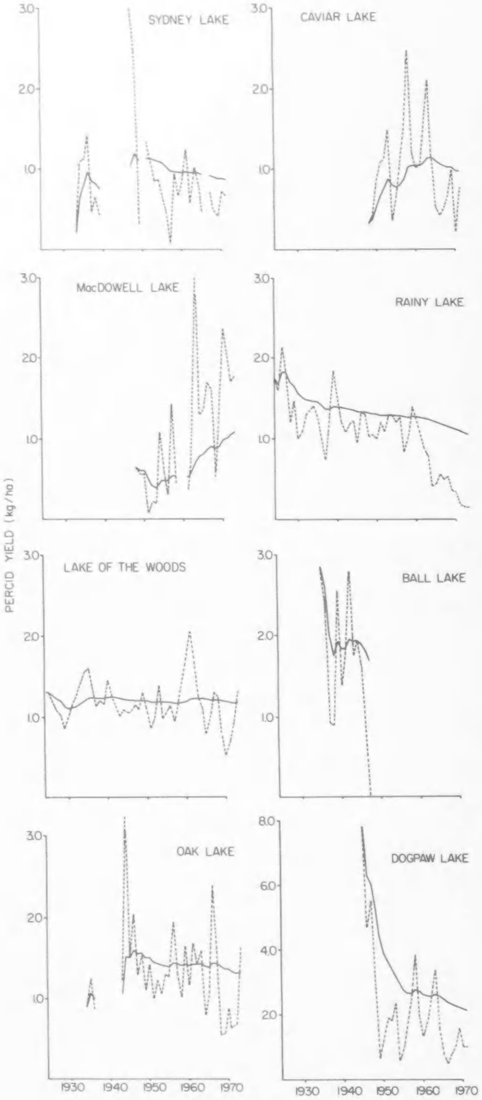

FIG. 3. Trends in commercial yields of percids, primarily walleye (*Stizostedion vitreum vitreum*), in eight lakes that had long-term percid yields greater than 0.85 $kg \cdot ha^{-1} \cdot yr^{-1}$. The broken lines represent annual yields and the solid lines represent cumulative average yields.

also noted this decline in walleye harvest and stated that walleye reported in the commercial catches declined from 30% of the total harvest in the mid 1920s to less than 10% in the late 1960s and early 1970s.

However, the observed decline in the commercial walleye catch in Rainy Lake, particularly in the last 10–20 yr, was probably not indicative of a decrease in the total walleye or percid harvest. Rainy Lake also has a substantial sport fishery for walleye. Although there are no published records of the angler harvest of walleye, tag returns (J. R. Chevalier personal communication) indicated that the walleye sport harvest equaled or exceeded that of the commercial harvest within the last decade. The total commercial yield in Rainy Lake exceeded the theoretical yield by an average of 37%. This apparent overexploitation was compounded by the substantial walleye harvest in the sport fishery — a fishery which traditionally is unregulated in terms of total harvest. Although sport and commercial walleye harvests from 1963 to 1973 may have been equivalent to commercial production in the late 1920s or throughout the 1930s, Rainy Lake is probably not capable of sustaining percid yields in the order of 1.80 $kg \cdot ha^{-1} \cdot yr^{-1}$.

For *Lake of the Woods*, percid yields (range of 0.52–2.06 $kg \cdot ha^{-1} \cdot yr^{-1}$) varied by less than 0.20 $kg \cdot ha^{-1} \cdot yr^{-1}$ (cumulative average) from 1924 to 1973 and was 1.18 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1973: the yields exceeded 1.0 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 40 of the 50 yr of record. Although the total commercial yield did not exceed the theoretical yield, as in Rainy Lake, the two lakes are similar in having a substantial walleye sport fishery. By 1940, it was estimated that angler harvest of walleye exceeded the harvest of this species by commercial fishermen (Macins 1972). Estimates by Macins (1972) from creel surveys indicated an angler harvest of walleye at 1.3–1.7 $kg \cdot ha^{-1} \cdot yr^{-1}$ from 1969 to 1971. This increasing angler harvest may, in part, account for larger fluctuations in the commercial harvest from 1960 to 1973 — a suggestion that the resiliency of the percid community was being pushed to its upper limits.

In *Oak Lake*, total commercial yield exceeded theoretical yield by an average of 16%. The long-term annual percid yields from 1943 to 1973 (range of 0.54 to 3.31 $kg \cdot ha^{-1} \cdot yr^{-1}$) declined to 1.32 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1973. Percid yields exceeded 1.00 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 25 of 34 fishing years but only once from 1968 to 1973.

The interpretation of the yield trend of percids from *Ball Lake* is difficult to assess because of the short duration of fishing (13 yr). However, in this period, the average yield of percids declined from 2.86 $kg \cdot ha^{-1} \cdot yr^{-1}$ in year one (1935) to 1.68 $kg \cdot ha^{-1} \cdot yr^{-1}$ in year 13 (1947). If the fishery had continued to operate, it is questionable whether percid yields of this magnitude could have been sustained, particularly since the yield of all species exceeded theroetical yield by an average of 38%.

Percid yields in *Dogpaw Lake* showed a classic example of fishing-up. From an initial yield of 7.85 kg/ha in 1945, the yields decreased to 0.68 kg/ha four years later and fluctuated until 1971. The yields exceeded 1.50 $kg \cdot ha^{-1} \cdot yr^{-1}$ only once from 1964 to 1971. As the total yield averaged 4½ times the theoretical yield, it is doubtful whether percid yields of 2.16 $kg \cdot ha^{-1} \cdot yr^{-1}$ (cumulative average) can be sustained. Dogpaw is a small lake (1,994 ha) and, as noted previously, there is an inverse relation between RYI and lake area in this set of 70 lakes.

Management Implications

In recognizing that selective exploitation may change the interspecific balance, management strategy in an intensive multispecies fishery must be to harvest each species proportional to its actual rate of protoplasmic elaboration if stability in the sense of community persistency is to be maintained in the system. Lacking stability, the standing crops of these species may fluctuate widely making it logistically difficult and more costly for commercial fishermen to operate. The magnitude of these fluctuations is dependent on community resiliency. Sustained populations ensure relatively uniform yields over time of the various species entering the fishery.

As indicated by the relation of RYI to theoretical yields in the 70 lakes, an increase in harvesting depends on a redistribution of effort over the available fish resource. As many of the lakes are relatively underexploited, full harvest potential might be attained through addition to the catch of underutilized species, such as sucker, burbot (*Lota lota*) and cisco (primarily *Coregonus artedii*). Support for this is found in Polish pikeperch (*S. lucioperca*) lakes, where Bonar (1977) described the influence of harvest of predatory species on total catch. In these Polish lakes, yield increased as the percentage of predatory species in the catch decreased.

Though addition to the catch of a previously underutilized species will raise the yield in many of the lakes, this management approach cannot be exercised on fisheries in which the RYIs are high. In these fisheries, any yield increase from underutilized resources will, in time, be offset by a decrease in total yield toward a new asymptotic level. Also, attempts must be made to reduce the risk of overexploitation on small, oligotrophic lakes where catchability appears to be inversely proportional to abundance.

Though it is recognized that management, in time, must understand the ecological interactions between species under a variety of exploitation regimes, the identification of regularities within the governing of community structure offers fishery science the opportunity to improve the present level of management. Identification of these regularities requires a recognition of emergent macrosystem properties (Kerr 1974) as components of community analyses. Long-term yield relations from the 70 lakes are variables observable at the community level and, as such, offer promise for experimental management.

The relation of percid yield to theoretical yield (average of 1:5) in the moderately to intensively fished lakes (RYI = 50 to 100%) reflects organizational structure and suggests a tentative proportioning of the MEI into a species (walleye) or community (percids) component. Though there is an obvious danger in utilizing averages, this relation may serve as a rough guideline for setting percid quotas in previously unfished boreal percid lakes.

The relation of percid yield to total yield appears to offer more promise for experimental managment as it was independent of RYI, lake productivity and lake area. Thus in boreal percid fisheries, with some history of catch records, percid harvest may approximate one-third of the total harvest. This relation is proposed to be an emergent property of this type of community. Bonar (1977) noted a similar relationship in Polish pikeperch lakes where percentage yield of predators attained a maximum at 25–30% of the total catch.

The functional relation of percid yield to the MEI suggests that an MEI range of 6–11 is optimum for walleye yields in boreal percid lakes (Fig. 4). As indicated previously, lakes in this range are considered mesotrophic to slightly eutrophic.

Implications from the data suggest that initially, community stability was high in most of the lakes, offering resistance to external perturbations. As energy fixed approached a balance with energy cost of maintenance, the rate of gross production (P) was low with high standing crop biomass (B) — hence, the high B:P ratio characteristic of equilibrium climax or a mature community (Odum 1969). Theoretically, the initial large catches of these fisheries was not based on turnover rates but was essentially from the standing crop (walleye and lake whitefish, primarily). Continual harvesting of these populations while generally not severe, reduced the system from equilibrium climax resulting in higher net community production partially at the expense of nutrient conservation, community diversity and, most importantly, community stability. With the concomitant loss of structural complexity in the macrosystem, there was a loss of the regulatory mechanism that dampened out fluctuations in species populations and prevented oscillations in inter-species systems. As the forces of homeostasis set in, the magnitude of population fluctuations was dependent on the intensity of stress (exploitation primarily) and the cybernetic efficiency of the system.

Other emergent properties of an unexploited percid community may include zero (or approaching zero) net community production. If so, then standing stocks are extremely vulnerable to exploitation by nature of their distributional patterns and resiliency is undoubtedly low because of the inherently low productive capacity of these waters. Implicit in the theoretical yield data for these lakes are primarily production rates that are limited by available nutrients. Possibly, nutrient removal in fish from a nutrient-limited system also can affect the rate of return to equilibrium climax.

In short, implications for management of commercial fisheries on boreal percid lakes offer three basic harvesting strategies. The first is a choice toward maximum production. This strategy, which over time can exceed the adaptive mechanisms of the system, results in a simplification of community structure which increases instability (the amplitude of population and species fluctuations) and decreases economic comfort to commercial fishing enterprises. The second choice is toward high community stability. Though this choice is obviously a strategy of nature (to return to equilibrium climax), the low turnover rates would offer little toward maintaining a commercial fishery. The third choice, the one recommended, is a compromise between biological and economic considerations and permits relatively heavy exploitation for 1 or 2 yr followed by a moratorium on fishing sufficient to allow the forces of nature to reassert themselves and the community to move once again toward equilibrium climax. This strategy appears to offer fishing enterprises a high turnover of biomass while still maintaining in the community a reasonable level of resistance to external perturbations.

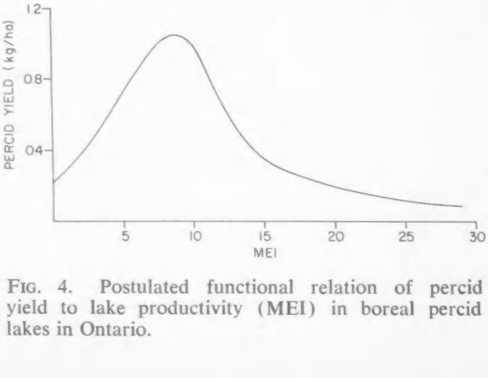

FIG. 4. Postulated functional relation of percid yield to lake productivity (MEI) in boreal percid lakes in Ontario.

Arctic char (*Salvelinus alpinus*) lakes in the Northwest Territories of Canada (L. Johnson personal communication) and salmonine and coregonine lakes in Lapland (H. Rundberg personal communication) traditionally have been fished in this manner. The capacity of northern lakes to return to a state of climax, provided that an adequate recovery period is given, has been demonstrated for a char population in Keyhole Lake (Hunter 1970; Johnson 1976). This recommended harvesting strategy would provide greater revenue to fishermen through a more economic operation on a time-invested basis. To maintain economic viability, this type of "pulse-fishing" would require a series of lakes for individual fishing groups which would be fished annually on a rotational basis. Recognizing that a rapid change in the density of any species population can alter interspecific balance and subsequent net reproductive success, care must be exercised in initiating and monitoring this type of harvesting strategy.

Although percids may be capable of forming up to one-third of the total yield, there is obviously an upper limit to sustainable yield. It is apparent that the yield of percids has exceeded this upper limit in Dogpaw Lake and a percid yield of 1.68 $kg \cdot ha^{-1} \cdot yr^{-1}$ in Ball Lake is also suspect. However, the yield of percids of 1.32 $kg \cdot ha^{-1} \cdot yr^{-1}$ in Oak Lake (cumulative average) has been relatively stable and has declined only slightly throughout the existence of the fishery.

The commercial yield of percids in Lake of the Woods has been consistent and currently averages about 1.20 $kg \cdot ha^{-1} \cdot yr^{-1}$. Rainy Lake, on the other hand, also with 50 yr of catch records, has shown a steady decrease in commercial yield, particularly in the last few years. Both Lake of the Woods and Rainy Lake have substantial sport fisheries for walleye. If, as indicated, the yield of walleye to anglers has approached or exceeded the commercial yield of the species, these lakes may now be yielding in the order of 2.0–2.5 $kg \cdot ha^{-1} \cdot yr^{-1}$. Those responsible for the management of these two lakes have expressed concern that walleye harvest has been excessive and corrective measures have been proposed to reduce the total annual yield of this species from these lakes.

Few northern Ontario lakes appear to be capable of sustaining percid yields greater than 1.50 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$. A sustainable yield of percids of 1.00–1.25 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ is probably a reasonable expectation for many moderately to intensively fished lakes in this region. Most lakes with long-term percid yields greater than 1.25 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ are likely to be considered as "problem" lakes and offer excellent opportunities for experimental management.

Acknowledgments

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Interrelations Between Walleye (*Stizostedion vitreum vitreum*) and Smallmouth Bass (*Micropterus dolomieui*) in Four Northeastern Minnesota Lakes, 1948–69[1]

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JOHNSON, F. H., AND J. G. HALE. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota lakes, 1948–69. J. Fish. Res. Board Can. 34: 1626–1632.

Smallmouth bass (*Micropterus dolomieui*) introduced from 1945 to 1948 into four rocky, infertile northeastern Minnesota lakes with established walleye (*Stizostedion vitreum vitreum*) populations reached maximum abundance in 9–15 yr and then declined to low numbers within 2–4 yr. In three, walleyes declined as the bass increased and in the fourth there was a simultaneous rise of walleye and bass followed by increased abundance of walleye with the decline of bass. Interspecific competition for spawning sites, shoal habitat, or food did not appear to be factors in the fluctuations in abundance. Growth of both species was density-dependent implying that intraspecific competition may have been the main factor. Also, predation of young walleye by bass may have been a factor in failure of walleye year-classes.

Key words: Percidae, species interrelations, *Stizostedion*, *Micropterus*, competition, diet, populations fluctuations, habitat use, density

JOHNSON, F. H., AND J. G. HALE. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota lakes, 1948–69. J. Fish. Res. Board Can. 34: 1626–1632.

Des achigans à petite bouche (*Micropterus dolomieui*) introduits entre 1945 et 1948 dans quatre lacs rocheux infertiles du nord-est du Manitoba contenant dejà des populations établies de dorés jaunes (*Stizostedion vitreum vitreum*) atteignirent un sommet d'abondance de 9 à 15 ans après, pour ensuite diminuer à un faible niveau en 2 à 4 ans. Dans trois lacs, les dorés jaunes diminuèrent à mesure qu'augmentèrent les achigans, et dans le quatrième, il y eut augmentation simultanée des dorés jaunes et des achigans suivie d'une augmentation des dorés jaunes avec le déclin des achigans. La concurrence interspécifique pour les frayères, les habitats peu profonds ou la nourriture ne semble pas avoir été des facteurs dans les fluctuations d'abondance. La croissance des deux espèces dépendait de la densité, ce qui donne à croire que la concurrence interspécifique a pu être le principal facteur. De plus, la prédation des achigans sur les jeunes dorés jaunes peut avoir été un facteur d'échac des classes d'âge des dorés.

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THE interrelations between smallmouth bass (*Micropterus dolomieui*) and walleye (*Stizostedion vitreum vitreum*) in four northeastern Minnesota lakes (Big, Hungry Jack, Pike, Two Island) were examined intermittently from 1948 through 1969 to determine the effects of bass introductions on established walleye populations in lakes in the area. Four possible factors in population changes were considered: spawning and spawning habitat, habitat use, food eaten, and growth and population density.

The lakes of the area (Table 1) lie on a southern extension of the Precambrian Shield. Here ancient bedrocks are exposed or lightly covered with reddish glacial till that is low in lime and soluble nutrients. Lake shores are mostly ledge rock, boulders, rubble, and gravel. Sand is uncommon. Mucky bottom is common in bays and beneath deep water. Aquatic macrophytes are usually absent on the rocky shoals of the main body but are present in moderately dense stands on the mucky or sandy bottoms of shallow bays. The climate is cool with ample rainfall. Most lakes have permanent outlets. Lake waters are

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] The original report of this study was prepared by the senior author before his death August 4, 1974. The present report, prepared by D. H. Schupp and W. J. Scidmore, is a revision of the original.

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TABLE 1. Some physical and chemical characteristics of the four study lakes.

			Type of bottom within 1.5 m contour (%)			Surface water chemistry (mg/ℓ)		
Lake	Area (ha)	Mean depth (m)	Ledge rock	Boulders and rubble	Sand, gravel, and muck	Total alkalinity[a]	Total phosphorus	Total nitrogen
Big	704.2	2.7	6	77	17	11.5	0.041	0.71
Hungry Jack	185.7	6.4	6	38	56	17.5	—	—
Pike	327.8	—	0	70	30	38.0	0.047	0.61
Two Island	321.3	3.0	0	95	5	12.6	0.010	1.15

[a] Potentiometric titration. Expressed as $CaCO_3$.

low in dissolved salts and relatively infertile, and general biological productivity is low (Moyle 1956). Fish populations are characterized by few species, low standing crops, and low angling yields.

Many of the lakes have long-established populations of walleye and are categorized by fish managers as softwater walleye lakes. Smallmouth bass were introduced into some of them, beginning in the 1920s, with the hope of increasing angling yield during the summer months (Surber 1924). Since then this species has become rather widely distributed by planting or migration.

Smallmouth bass were introduced in the study lakes between 1945 and 1948. The first introductions were small in number and were followed with the next 1–5 yr by larger plants. None have been stocked since.

In addition to the walleye, the common sucker (*Catastomus commersoni*) and yellow perch (*Perca flavescens*) were the only species present in abundance in all lakes. Other large species found in small numbers in one or more of the lakes were northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), green sunfish (*Lepomis cyanellus*), bluegill (*Lepomis machrochirus*), and whitefish (*Coregonus clupeaformis*). Small fishes found in small numbers in one or more of the lakes were the Iowa darter (*Etheostoma exile*), Johnny darter (*Etheostoma nigrum*), central mudminnow (*Umbra limi*), bluntnose minnow (*Pimephales notatus*), brook stickleback (*Eucalia inconstans*), mottled sculpin (*Cottus bairdi*), and blacknose dace (*Rhinicthys atratulus*).

Materials and Methods

Population trends of walleye and smallmouth bass were determined from numbers of fish per lift in nylon gillnet (76.2 × 1.8 m with five 15.2 m sections of 3.8, 5.1, 6.4, 7.6, and 9.1 cm stretch mesh) sets made at irregular intervals in the study lakes from 1948 to 1969. The number of sets in the years netted varied from 2 to 16 per lake. All sets were overnight and made in July or August in areas where experience had shown walleye and smallmouth bass were likely to be found.

Diel occupations of shoal areas by walleye and smallmouth bass were determined by night electrofishing with a 230 V, a-c generator in late May, late June and mid-July in Big and Hungry Jack lakes (1959–60) and by comparison of catches of these species in 390 daytime (0800–2000 h) and 387 nighttime (2000–0800 h) trapnet sets in Pike Lake in 1962. Eight to 10 trap nets (0.9 × 1.8 m frame and 15.2 m leads with 5.1 cm stretch mesh in leads and pot) were fished daily at inshore locations on different bottom types from June 13 to August 28.

Kinds and amounts of food ingested by 470 walleye and 489 smallmouth age I and older taken in the trap nets at Pike Lake was obtained by use of a stomach pump (Seaburg 1957). Frequency occurrences of ingested food items were recorded by major types (fish, crustaceans, leeches, and insects) in the field and food volumes were measured in the laboratory from composite weekly samples for each species.

Habitat preferences were determined by direct observation, trap netting, and electrofishing.

Scales examined for age-and-growth were taken from fish obtained mostly in gill and trap nets. Growth was calculated from magnified scale impressions (40×) using a direct proportion nomograph.

Fish Population Trends

Smallmouth bass populations gradually increased to a peak 9–15 yr after introduction and then declined to low levels in 2–4 yr (Fig. 1). Catches in experimental gill nets from 1948 to 1969 indicate that in three of the four lakes (Big, Hungry Jack, Two Island) the walleye population generally declined as the bass population increased. The numbers/lift of walleye in these lakes when bass abundance was greatest were significantly lower (Mann–Whitney) test) than the catches when bass were less abundant (Table 2). In the fourth lake (Pike Lake) net catches of

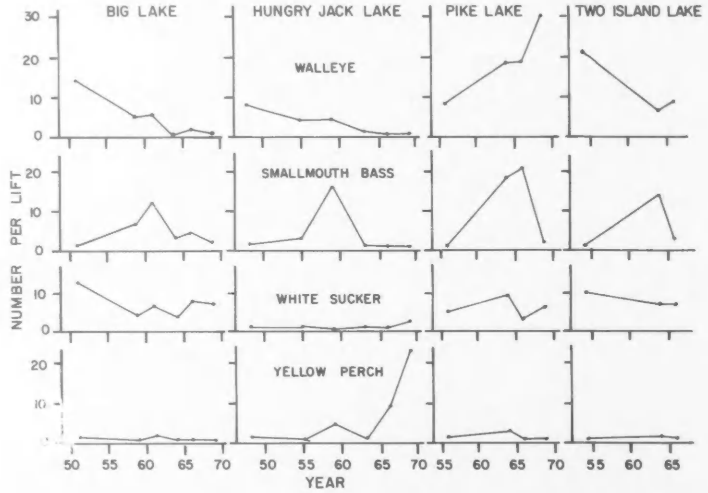

FIG. 1. Mean numbers of walleye, smallmouth bass, white sucker, and yellow perch per gillnet lift from Big, Hungry Jack, Pike, and Two Island lakes, 1948–69.

walleye and bass rose simultaneously between 1955 and 1966, after which bass declined and walleye continued to increase.

The age-class distributions in Big Lake (Fig. 2) suggest that the decline of the walleye population resulted from poor survival (or production) of young-of-the-year in several successive years when bass were increasing in abundance. Small year-classes in 1956, 1959, and 1962 coincided with the only years of stocking. Older walleyes (ages VII and older) tended to predominate in the net catches from 1959 to 1969 indicating poor survival of young in earlier years. Smallmouth bass had more age-classes represented throughout the study period. Much of the gillnet catches consisted of fishes of ages III and IV indicating more consistent survival of young and recruitment to the population than was the case for walleyes.

Similar relationships were observed in Hungry Jack and Two Island lakes. Walleye recruitment was low in Hungry Jack Lake. No representatives of the 1954 to 1957 year-classes were present in the small sample taken in the 1959 gill nets. The catch of walleye by anglers in 1959 was also low. Only 7% of the catch were walleye, the remainder being bass (R. C. Micklus, MN. Dep. Nat. Res. unpublished data). Resort owners reported that the catches before 1955 were primarily of walleye. In Two Island Lake, walleyes decreased from 1954 to 1964 and after the bass population declined walleyes increased slightly (Table 2).

There was a more nearly regular distribution of walleye year-classes in Pike Lake (Fig. 2) than in the other lakes. Gillnet and the 1962 trapnet catches were mostly of fish of ages III and IV. Though catches of both smallmouth and walleye rose from 1955 to 1966 (Table 2) there were evidently four successive poor walleye year-classes during this period despite walleye stocking in 1962 (Fig. 2).

Factors in Population Fluctuations

Spawning and spawning habitat — No overlap in the periods of spawning and selection of spawning and selection of spawning sites by walleye and smallmouth bass was found in the two lakes (Big, Pike) where spawning activities were observed. Much of the apparently suitable spawning area was not used by bass suggesting that availability of spawning habitat was not a factor in the increase or decline of the bass population.

In the two lakes, walleye spawned during the first 2 wk in May shortly after ice had left the lakes when water temperatures were 6.7–8.9°C Smallmouth bass spawned 3–4 wk later when water temperatures were between 12 and 20°C. Walleye spawning took place mostly on rocky shoals in the main basin of the lakes, especially on exposed, wave-washed shores and points where there was clean gravel and rubble, while smallmouth nests were usually in sheltered areas in bays or behind islands. In general, spawning sites were similar to those described for other waters for smallmouth bass (Beeman 1924;

TABLE 2. Numbers of walleye and smallmouth bass ages I and older per gillnet lift after introductions of bass in four northeastern Minnesota lakes studied intermittently from 1948 to 1969.

Year	Number of lifts	Walleye N/lift	Smallmouth bass N/lift
		Big[a]	
1951	12	15.1(3–29)[b]	0.6(0–2)[b]
1959	8	5.5(0–18)[c]	6.9(4–9)[c]
1961	8	6.8(1–16)	13.0(8–22)
1964	8	0.8(0–3)[c]	3.1(0–8)[c]
1966	8	2.6(0–6)	5.4(0–16)
1969	16	1.0(0–3)	2.4(0–7)
		Hungry Jack[a]	
1948	9	8.0(4–12)	2.2(0–6)
1955	9	4.8(1–15)[c]	4.2(1–8)[c]
1959	2	5.0(3–7)	16.5(2–31)
1963	15	1.3(0–5)	0.8(0–5)
1966	16	0.4(0–2)	0.3(0–2)
1969	5	1.0(0–3)	0.6(0–1)
		Pike[a]	
1955	12	6.8(0–16)	1.4(0–5)
1964	8	18.5(7–32)[c]	18.4(2–37)[c]
1966	4	18.5(15–22)	20.2(6–44)
1969	4	32.0(13–55)	2.0(1–4)[c]
		Two Island[a]	
1954	7	21.4(4–38)	1.4(0–3)
1964	8	6.8(2–18)[c]	14.5(6–24)[c]
1966	8	9.4(3–26)	2.6(2–5)

[a] Introductory stockings of smallmouth bass fingerlings by years and number per hectare as follows: Big Lake, 1945 — 0.3, 1946 — 9.5, 1949 — 4.8; Hungry Jack, 1945 — 3.4, 1950 — 79.1; Pike, 1947 — 1.2, 1948 — 1.5, 1951 — 45.8; Two Island, 1948 — 1.9, 1951 — 31.1.

[b] Range.

[c] Difference in number/lift between years significant (Mann–Whitney T) $P < 0.05$.

Tester 1930; Langlois 1932; Latta 1963) and walleye (Eschmeyer 1950; Johnson 1961).

There were fewer smallmouth nests in these lakes than might have been expected from the size of the lakes, abundance of bass, and amount of apparently suitable spawning area. Several searches in Big Lake (704 ha, shoreline 27.2 km) yielded only about 125 nests.

Spawning walleyes or their eggs were observed on nearly all suitable spawning areas.

Habitat use — Smallmouth bass appeared to frequent a wider variety of bottom types than did walleye. They were about equally abundant on inshore areas during both day and night while the walleye exhibited a diurnal pattern of movement.

Walleye appeared to prefer bottoms of finer soils where there was some vegetation to rocky

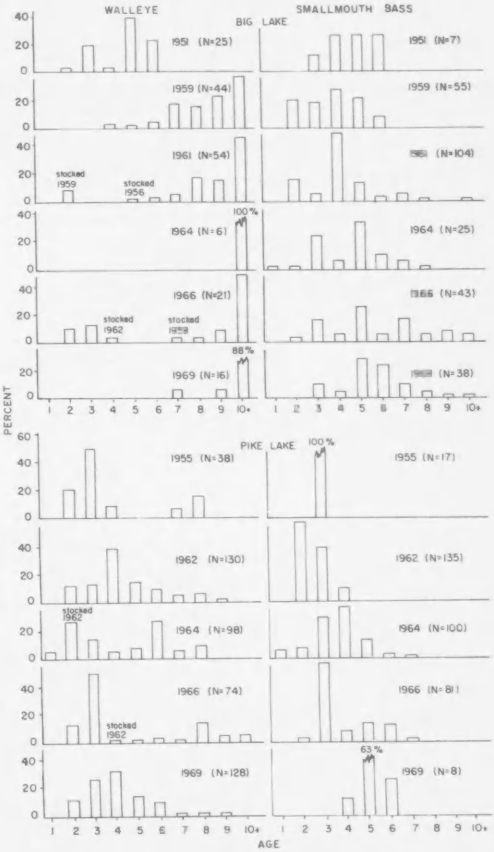

FIG. 2. Age-class distribution (percentages of total catches) of walleye and smallmouth bass caught in gill nets from Big and Pike lakes and in trap nets from Pike Lake in 1962.

TABLE 3. Mean catches of age 1 and older smallmouth bass, walleye, and associated species per 5 min of night electrofishing over shoals of different bottom types in Big and Hungry Jack lakes, 1959–60[a].

Bottom type	Small mouth bass	Walleye	White sucker	Yellow perch
Ledge rock–boulders	5.60	0.00	0.10	0.00
Boulders–rubble	5.33	0.03	0.01	0.00
Sand–gravel–few boulders	1.40	0.14	1.30	1.40
Muck–few boulders	2.17	0.08	0.67	0.01

[a] Total minutes fished: Big Lake, 615; Hungry Jack, 210.

TABLE 4. Occurrence of food items in stomachs of 470 walleye and 429 smallmouth bass age 1 and older taken from Pike Lake from June 13 to August 28, 1962.

Food type	Age or stage	Walleye		Smallmouth bass	
		Percent occur.	Percent of total stomach volume	Percent occur.	Percent of total stomach volume
Fish (all species)	0		3.0		2.4
	1+		40.2		15.4
	Both	26	43.2	16	17.8
Yellow perch	0		1.2		0.1
	1+		21.3		1.0
Walleye	0		0.1		0.7
	1+		0.2		1.8
Minnows	1+		0.1		0.1
Sucker	1+		10.9[a]		0.0
Sculpin	1+		1.1		8.1
Stickleback	1+		0.4		0.2
Darters	1+		0.2		0.1
Unidentified	0		1.7		1.6
	1+		6.0		4.0
Insects (all species)	Adult	19	0.2	27	4.6
	Immat.	60	30.6	45	17.2
	Both	79	30.8	72	21.8
Ephemoptera	Adult		0.0		2.4
	Immat.		22.2		3.8
Diptera	Adult		0.2		trace[b]
	Immat.		0.6		trace
Odonata	Adult		trace		0.9
	Immat.		6.3		11.1
Other or unidentified	Adult		trace		1.3
	Immat.		1.5		2.3
Crayfish	—	47	18.0	60	49.5
Leeches	—	9	3.0	14	9.4
Crustacea other than crayfish	—	9	2.0	4	1.5
Vegetation	—	10	3.0	2	trace

[a] In stomach of one fish.
[b] Less than 0.1%.

and boulder covered bottoms — at least at night when inshore. Smallmouth, although found on bottoms of finer soils, were taken mainly on rocky and boulder-strewn shoal areas. Night catches of fish (ages 1 plus) by electrofishing showed more walleyes, and yellow perch on sandy and mucky bottomed areas, where there were few boulders, than on shoals of ledge rock and boulders. The converse was true for smallmouth bass (Table 3). Similar habitat preferences by walleye were found in Pike Lake by trap netting in 1962 but smallmouth were about equally abundant on the two kinds of bottom. Perch, which are the main food of young walleye in more fertile walleye lakes, were found mostly in the weedy bays and not on the rocky shoals.

As reported in other studies (Carlander and Cleary 1949; Rawson 1956), walleye were more active at night and moved inshore. Catches of walleye in trap nets in Pike Lake in 1962 were markedly higher in the overnight sets than those fished during daylight hours: 1.47 and 0.05 fish per lift, respectively. There was little difference in the catches of smallmouth bass in the two series of sets the average being 0.73 and 0.78 bass per lift.

Foods eaten — Diets of the walleye and bass were similar in Pike Lake, the one lake studied, but there were considerable differences in the kinds and growth stages of organisms eaten and differences in the periods of peak consumption.

During the period studied (June 13–August 28) the two species evidently utilized the same kinds of foods, but walleye fed mostly on fish and smallmouth fed mostly on crayfish (Table 4). Both utilized insects extensively but walleye fed most heavily on immature mayflies (22%

TABLE 5. Mean calculated total lengths and ranges at each annulus of age I–IV walleye and smallmouth bass in Big and Pike lakes when populations of the two species differed notably in abundance.

Growth period	Year-classes present in period	Estimated relative abundance	Length (cm)			
			I	II	III	IV
			WALLEYE			
			Big Lake			
1945–53	1945–49 1952, 1953	High	12.1(62)[a] 8.6–17.3[b]	18.9(62) 12.4–25.1	23.9(54) 16.8–31.0	28.9(54) 21.8–35.1
				—[c]	—[c]	—[c]
1957–66	1957, 1958, 1959, 1960, 1962	Low	11.9(13) 9.1–17.3	25.0(13)[c] 21.3–30.5	34.1(7)[c] 29.2–39.6	37.7(5)[c] 35.8–38.6
			Pike Lake			
1949–55	1949–54	Low to moderate	9.2(88) 6.1–13.2	21.1(88) 15.7–27.9	28.9(88) 22.3–39.6	35.6(47) 30.0–44.9
				—[c]	—[c]	—[c]
1966–69	1965–68	High	7.6(51) 5.6–14.7	17.1(91) 13.7–24.1	25.9(76) 21.1–30.0	32.1(78) 28.9–35.6
			SMALLMOUTH BASS			
			Big Lake			
1946–50	1946–49	Low	6.8(7) 6.1–8.1	13.5(7) 11.7–14.5	19.3(6) 18.0–21.8	24.1(4) 21.8–25.9
				—[c]	—[c]	—[c]
1957–61	1957–61	High	6.8(95) 4.6–9.1	11.8(97) 7.6–15.7	16.7(63) 10.9–19.3	21.6(43) 18.8–24.4
			Pike Lake			
1953–61	1953, 1958, 1959, 1960, 1961	Low to moderate	6.4(185) 4.6–11.7	14.3(161) 9.4–19.6	23.4(75) 15.7–31.2	28.4(13) 23.4–33.0
				—[c]	—[c]	—[c]
1962–66	1962–66	High	6.4(95) 4.1–8.9	12.6(71) 8.6–20.3	18.2(63) 14.5–30.2	24.7(7) 21.6–30.0

[a] Number in sample.

[b] Range.

[c] Difference in mean calculated total length at each age in years of low and high abundance also significant ($P < 0.05$) when variances are not assumed the same (Snedecor and Cochran 1967., p. 115).

of total food volume) whereas smallmouth fed most heavily on immature odonates (11% of total food volume). The bass also took some mayflies, both immatures and adults.

In terms of percentage occurrence of food items in the stomach, insects rated highest for both walleye and bass followed in descending order by crayfish, fish, and leeches.

Crayfish were prominent in the diet of bass throughout the summer but were not utilized by walleye extensively.

Yellow perch made up 21% of stomach contents of age I plus walleye. In the bass stomach volumes, perch were exceeded by both sculpins and walleye, 8.1 and 1.8% of the food volume, respectively. In the more fertile Minnesota walleye lakes, perch especially young-of-the-year perch make up a major portion of the diet of walleye (Maloney and Johnson 1955; Dobie 1966; and Johnson 1969).

Although the incidence of walleye in bass stomachs was low, predation by a large population of bass may have influenced walleye fingerling survival.

Growth and population density — The growth of walleye and bass from age II through age IV was density-dependent in both Big and Pike Lakes (Table 5).

Density-dependent growth was not indicated for age I walleye and bass in Big Lake. At Pike Lake, age I walleye were significantly smaller at high population abundance but no difference was found in size of age I bass in relation to population density.

General Discussion

The decline of walleye in three of the four study lakes was coincident with the expansion of the bass populations. The reduction in walleye recruitment as bass abundance increased suggests that losses of young walleye increased with the increase in bass numbers. Although there was some predation by bass on walleye, this occurred in the fourth study lake (Pike Lake) where walleye and bass populations increased simultaneously.

If interspecific stresses were involved in the relationships observed, they were not detected, suggesting that the fluctuations in populations were independent.

Interspecific competition (here defined as the demand at the same time of more than one organism for the same resource of the environment in excess of immediate supply; from Larkin 1956) for food between walleye and smallmouth bass was probably not the principal factor influencing the abundance of either species. Both species exhibited considerable versatility in their selection of food organisms. A similar conclusion was drawn by Fedoruk (1966), who studied walleye and smallmouth bass feeding relationships in Falcon Lake, Manitoba. There, as in Pike Lake, crayfish made up much of the bass diet throughout the summer while that of the walleye was mainly of ephemerid nymphs and fish.

Analysis of growth rate and food consumption suggests that intraspecific competition for food was the most important factor influencing the growth and abundance of bass in the study lakes and was also an important factor in walleye growth.

From the data available, we cannot determine the factors that caused the sharp drop in bass populations after their buildup to a high level. The marked reductions within 2–4 yr after peak populations were reached would be expected when a species increases substantially above carrying capacity and various mortality factors intervene to check population growth.

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Responses of Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*) Populations to Removal of White Sucker (*Catostomus commersoni*) from a Minnesota Lake, 1966[1]

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JOHNSON, F. H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34: 1633–1642.

In a northeastern Minnesota lake subject only to sportfishing, removal of 85% of the estimated standing crop (34 kg/ha) of adult white suckers, *Catostomus commersoni*, in 1966 was followed by marked changes in community structure and interrelations. During 7 yr after the removal: catch indices for adult suckers remained far below those before the sucker removal but juvenile suckers increased about 17-fold; yellow perch, *Perca flavescens*, increased about 15-fold; walleye, *Stizostedion vitreum vitreum*, standing crop increased about one-third; mayflies increased in diet of adult perch and smaller invertebrates decreased; micro-crustaceans increased in diet of young-of-the-year and juvenile perch; young-of-the-year perch increased in diet of adult walleye; walleye angling yield increased from an average of 3.0 kg/ha before the removal to an average of 4.9 kg/ha in 1970–73; the rate of exploitation of adult walleye did not change with increase in angling effort; and the increased walleye harvest consisted mostly of fish recruited to the catch during the fishing season. The average annual harvest of walleye in 1970–73 exceeded estimated potential production for all fish by 81.5% and probably cannot be sustained. Removal of white suckers from lakes with limited fish species diversity appears to benefit percid populations.

Key words: Percidae, species interactions, (*Stizostedion vitreum vitreum*), *Perca flavescens*, *Catostomus commersoni*, harvests, community response, community ecology, food, competition

JOHNSON, F. H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34: 1633–1642.

Dans un lac du nord-est du Minnesota où il ne se pratique qu'une pêche sportive, l'enlèvement de 85% de la biomasse estimée (34 kg/ha) de meuniers noirs adultes, *Catostomus commersoni*, en 1966 fut suivi de changements marqués dans la structure et les relations mutuelles de la communauté. Au cours des 7 années qui suivirent l'enlèvement: les indices de capture de meuniers noirs adultes demeurent de beaucoup inférieurs à ceux d'avant l'enlèvement des meuniers noirs, mais les jeunes meuniers noirs augmentent d'environ 17 fois; la perchaude, *Perca flavescens*, augmente d'environ 15 fois; la biomasse de dorés jaunes, *Stizostedion vitreum vitreum*, augmente d'environ un tiers; les phryganes augmentent dans le régime alimentaire des perchaudes adultes, et les invertébrés plus petits diminuent; les microcrustacés augmentent dans le régime des perchaudes de l'années et des perchaudes un peu plus âgées; les perchaudes de l'année augmentent dans le régime des dorés jaunes adultes; les dorés jaunes capturés à la ligne augmentent d'une moyenne de 3.0 kg/ha avant l'envèvement à une moyenne de 4.9 kg/ha en 1970–73; le taux d'exploitation des dorés jaunes adultes ne change pas avec l'augmentation de l'effort de pêche à la ligne; et la récolte accrue de dorés jaunes consiste en grande partie en poissons qui sont devenus pêchables durant la saison de pêche. La récolte annuelle moyenne de dorés jaunes en 1970–73 dépassait de 81.5% la production potentielle estimée de tous les poissons

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] The author had completed field work and much of the data analysis before his death August 4, 1974. The data analysis was completed and the report prepared by T. C. Osborn, D. H. Schupp, and W. J. Scidmore.

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et ne peut probablement pas se maintenir au même niveau. L'enlèvement des meuniers noirs des lacs dans lesquels la diversité des espèces de poissons est limitée semble favoriser les populations de percidés.

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IN this study, 1964–73, the removal of white sucker, *Catostomus commersoni*, was evaluated as a method for increasing populations of yellow perch, *Perca flavescens*, and walleye, *Stizostedion vitreum vitreum*, in Wilson Lake. Interspecific relations of these and associated species were examined to better define the role of the white sucker in the rocky infertile lakes, with low species diversity, in northeastern Minnesota.

The white sucker usually makes up a substantial part of the fish community in these lakes. It had been observed that the near elimination of the adult sucker population from a 105 ha lake trout–rainbow trout lake in northeastern Minnesota was followed by a marked increase in abundance of yellow perch and the lake chub, *Couesius plumbeus* (Unpublished data, Section of Fisheries, Minn. Dep. Nat. Res.). The increase in the perch population suggested that reduction of suckers might benefit walleye if perch, a preferred prey species, increased in abundance.

Similar responses have been noted in Poland where removal of bream, *Abramis brama*, was followed by an increase in abundance of roach, *Rutilus rutilus*, a food source for pikeperch, *Stizostedion lucioperca*, and an increase in the population of pikeperch (A. Bonar, Academy of Agriculture and Technology, Institute of Icthyobiology and Fisheries, Olsztyn, Poland, personal communication). Olson (1963) and Dobie (1966) indicated that suckers were not an important food of walleye in Minnesota lakes but might compete with walleye for invertebrate foods, particularly immature insects.

Wilson Lake was selected for study because it had a reputation for good walleye fishing, its fish population contained few species with walleye and sucker predominating, and is typical of many northeastern Minnesota lakes. In addition it is a headwater lake with few tributaries, and an outlet dam prevents upstream migration of fish into the lake.

The study was conducted in three phases: (1) from May through September of 1964 and 1965, basic data were obtained on fish life histories, fish population and invertebrate abundance, and the angling catches; (2) intensive sucker removal by trapnetting in the spring of 1966; and (3) measurement of the responses of fish from May through September, 1967–73. No fish stocking or other fish management was undertaken during the period of study, but the access road was widened and improved in 1970.

Lake Description

Wilson Lake (Fig. 1) is located in the Precambrian shield region of northeastern Minnesota. It has four small intermittent inlets, three from swamp drainage and one from Little Wilson Lake, about 100 m upstream. The outlet is tributary to the Cross River, which drains into Lake Superior.

During much of the open water season the lake is homothermous and water temperatures vary by only 2 or 3 deg. C from surface to bottom. Maximum surface temperature recorded during the study was 25°C. Physical and chemical characteristics of the lake are given in Table 1.

Four species of fish were taken in gill nets set in 1964 and 1965. In order of abundance these were: walleye, white sucker, yellow perch, and northern pike (*Esox lucius*). Catches in a 1954 lake survey consisted of the same species; catch rates of walleye and yellow perch were similar to those in 1964–65 but sucker abundance was greater (Unpublished data, Section of Fisheries, Minn. Dep. Nat. Res.).

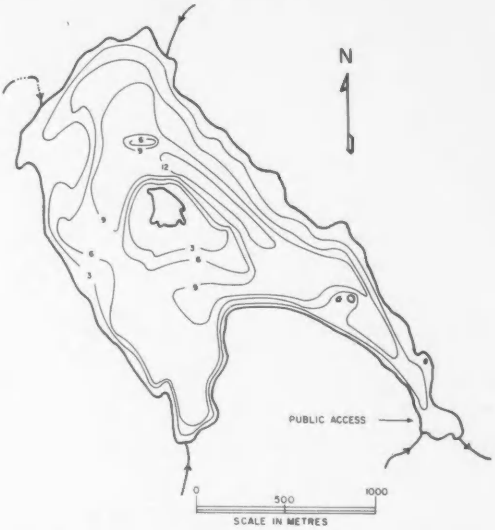

FIG. 1. Wilson Lake, Lake County, Minnesota. Contours in metres.

TABLE 1. Physical and chemical characteristics of Wilson Lake.[a]

Latitude	47°37′ N	Transparency (secchi disc)	2.5–5.2 m
Longitude	90°58′ W	Total dissolved solids	31.6 mg/ℓ[b]
Area	245 ha	Total alkalinity	23.0 mg/ℓ (15.0–32.5)[c]
Volume	63×10^7 m^3	Total phosphorous	0.03 mg/ℓ (0.02–0.07)
Mean depth	6.6 m	Total Kjeldahl nitrogen	0.47 mg/ℓ (0.27–0.62)
Max. depth	14 m	pH	8.0 (7.8–9.3)
Morphoedaphic index 4.8			

[a] Water chemistry data, except TDS, from composite surface samples taken in June, July, and August in 1964, 1965, and 1967.

[b] TDS from a composite surface sample July 1976.

[c] Range.

Collections of small fish and minnows were mainly Iowa darter (*Etheostoma exile*), Johnny darter (*Etheostoma nigrum*), and bluntnose minnow (*Pimephales notatus*). Also present were mottled sculpin (*Cottus bairdii*), blacknose shiner (*Notropis heterolepis*), longnose dace (*Rhinichthys cataractae*), and the pearl dace (*Semotilus margarita*).

Emergent macrophytes were limited to beds of yellow waterlily (*Nuphar* sp.) on soft bottom in bays. The most common submerged macrophytes were variable pondweed (*Potamageton gramineus*) and bushy pondweed (*Najas flexilis*) on offshore sandy shoals to depths of about 3.5 m. Beds of bladderwort (*Utricularia* sp.) occurred to a depth of 6 m. Aquatic plants were absent along the rubble shorelines.

Materials and Methods

Limnological studies — Composite surface water samples from several areas were collected in June, July, and August 1964–65 and 1967 and analyzed for total alkalinity, total phosphorus, total Kjeldahl nitrogen and pH, using standard methods (APHA et al. 1946). Water temperature and dissolved oxygen profiles, and water transparency (secchi disc) were obtained from the deepest area of the lake.

Weekly plankton tows of 76 m were made with a 25.4 cm diameter townet of Number 6 nylon mesh at each of four stations from early May through August in 1964–65 and 1967 at depths of 1.5 and 3 m. Settled volumes of crustacea and algae were measured by the method of Dobie and Moyle (1956). Counts of preserved samples were made in a Sedgewick–Rafter cell.

Bottom fauna were sampled with a 15.2 cm Petersen dredge at biweekly intervals from June through August, 1964 through 1970, at the six summer trapnetting stations used for food consumption studies. Samples were taken at 1–2 and 5–6 m and quantities of organisms were expressed as numbers and volume per square meter.

Fish population studies — Fish were netted with three types of gear: (1) a 12.2 × 1.5 m bag seine with 6.35 mm bar mesh, and a 9.1 × 1.2 m bobbinet seine; (2) a 36.2 × 1.8 m nylon sampling gill net containing five 15.2 m graduated sections and a 15.2 m nylon gill net with 3.8 cm stretch mesh; and (3) standard Minnesota trap nets with 15.2 m leads and 6.1 cm stretch mesh in both lead and pot.

Fish abundance indices (numbers/lift) of walleye, suckers, perch, and northern pike were based on overnight gillnet catches at six stations netted in early September from 1964 through 1973. Captured fish were measured, weighed and sexed.

Relative abundance of young-of-the-year (hereafter referred to as "young") and other small fish was determined by biweekly seining at four stations during July and August 1964 through 1973.

Ages of fish were determined from scale impressions. Growth was back-calculated using a direct proportion nomograph. Only the last 2 complete yr of growth were used to calculate growth increments.

The condition factor (K) was calculated for male walleye captured each spring in 1964–65 and 1969–73, and for yellow perch in the summers of 1965, 1967, and 1970.

Petersen type population estimates (Ricker 1975) were made for walleye larger than 305 mm and mature white suckers caught by trap netting in spring and marked with either a finclip or an anchor tag.[3] The angling catch was examined for walleye recaptures and estimates were corrected for recruitment by using growth increments for age IV and V walleye. White suckers were recaptured by trap nets during the spawning season and summer trap netting.

The annual mortality rate for adult walleye was estimated from returns of marked walleye in spring trap netting the first 2 yr after marking, and from the age-class distribution of the sportfishing catch. The rate of exploitation for adult walleye was estimated in 1965 and each year from 1969 through 1973 from marked fish caught by angling.

Food studies — Foods of adult walleye, yellow perch, and northern pike were determined from stomach contents obtained with a stomach pump (Seaburg 1957) from live fish captured in trap nets at six stations netted 3–4 days per week from May 15 through Aug. 31 in 1964–65 and 1967 and 1970. Food of adult suckers was determined in 1964 and 1965 only from contents of entire digestive tracts.

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[3] Floy Tag Co., Seattle, Washington 98105, Catalog No. FD 67E. Mention of brand names does not constitute endorsement of product.

Kinds and sizes of fish too small to be sampled by trap nets were obtained with small mesh gill nets or seines and preserved for laboratory analysis.

Frequencies of occurrence of major food types (Crustacea, leeches, insects, fish) were recorded as each fish was examined. Samples of food from each species were composited weekly and food volumes and number of organisms were determined in the laboratory.

Food items used by two or more species on the same day were tabulated. If frequency of occurrence for one food item exceeded 25% for two or more species it was considered an indication of potential competition.

Food consumption data from trapnet-caught fish were used because a comparison of food items and their relative abundance in the stomachs of fish captured in trap nets and in gill nets during the fall netting period showed the compositions of the diets, and changes in diets, were essentially the same for fish captured in the two kinds of gear. Trap netting was the only practicable method of capture available; use of seines or trawls was precluded in much of the lake by the nature of the bottom and season-long gill netting would have destroyed too many fish.

Foods eaten by yellow perch and walleye for the 2 preremoval yr were combined as was the data for the 2 postremoval yr to minimize the effect of variation between years in the abundance of individual organisms. Sample sizes large enough for comparison of walleye foods in both periods were available only for young walleye and those larger than 229 mm.

Creel census — Creel census was conducted on a 4-day-on, 4-day-off schedule from opening of the season in mid-May through September or into early October for all years of the study except 1966 and 1968. Tallied catch data were expanded directly to total fishing days to estimate fishing pressure and catches. The catches of marked walleye were estimated in the same manner.

Sucker removal — Adult white suckers were removed by trap netting beginning immediately after ice-out (May 21) in 1966. From May 21 to June 3, 5369 adult suckers weighing 7076 kg (85% of the etsimated spring standing crop) were removed (Johnson 1975). Removal was continued each spring in succeeding years to capture as many of the remaining adults as possible.

Effects of White Sucker Removal

FEEDING INTERRELATIONS

The diets of fishes in the lake before sucker removal indicated a number of areas where competition for food might occur, particularly for invertebrates. After removal a complex series of interrelated changes in foods eaten occurred (Fig. 2).

The white sucker, yellow perch, walleye, and various minnows and darters were the primary consumers of invertebrates. Of these, the white sucker was the species most frequently involved in potential competition for food items.

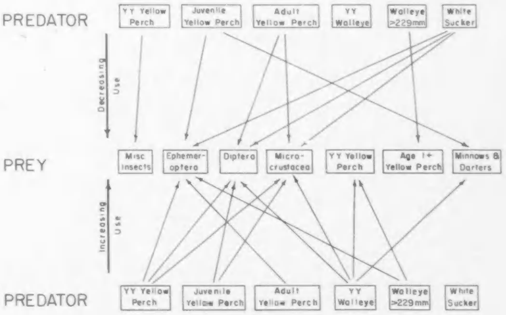

FIG. 2. Major changes in feeding interrelations of selected predator groups after sucker removal, based on changes in items consumed before removal (1964–65) and after removal (1967 and 1970), Wilson Lake.

White suckers fed almost exclusively on invertebrate foods, mainly immature insects (Table 2). Most common among these were larval midges (Chironomidae) and mayfly nymphs (mostly *Hexagenia sp.*). These two groups contributed 25.4 and 43.7%, respectively of the identifiable animal foods found in sucker stomachs. Micro-crustaceans, mainly amphipods and Cladocera, were the only other noteworthy food items.

The most commonly observed instances of potential competition were between suckers and yellow perch, occurring 16 times in a total of 53 observations. The 16 observations of white sucker–yellow perch potential competition were 69.6% of those in which perch were involved.

TABLE 2. Food of white sucker 40 cm and larger (587 fish) expressed as mean volume (ml) per fish and percent of total for each food item, Wilson Lake, 1964–65.

Food item	Mean volume	% total volume	% identifiable animal foods
Crustacea	0.173	7.6	14.4
Insecta	1.007	44.5	83.8
Diptera	0.305	13.5	25.4
Ephemeroptera	0.525	23.2	43.7
Other	0.177	7.8	—
Mollusca	0.021	0.9	1.7
Unidentified	0.962	42.5	
Sand & vegetation	0.099	4.4	
Total	2.262		

Similarly, the sucker was involved in 68–80% of the instances of potential competition where minnows, walleye, or darters were the other consumer (Johnson 1975). Thus the sucker appeared to be a potential competitor for food with walleye, the primary piscivore, and with the most important prey fishes in the lake.

Before removal, micro-crustaceans were prominent food for perch of all sizes, but were most prominent in the diet of young perch, making up 63.8% of the volume of food consumed. These organisms made up 43.1% of the diet of perch 51–127 mm and 35.6% of the diet of perch larger than 127 mm. After sucker removal, the mean volume of crustaceans consumed by the largest perch was less than 10% of the preremoval volume and made up only 3.7% of all foods consumed. Yellow perch in the intermediate size range, 51–127 mm, increased consumption of crustaceans by about one-third in the postremoval period. The mean volume of crustaceans in young perch also increased by one-third after sucker removal (Table 3).

Reduced consumption of crustaceans by large perch (>127 mm) was offset by a corresponding increase in use of mayflies. The mean volume of mayflies in the diet of these perch increased by 2.5 times and the difference between the pre- and postremoval mean volumes was 0.114 ml, nearly the same as the 0.117 ml decline in volume of crustaceans. Mayflies made up 57.8% of the food volume of large perch after removal compared with 19.7% before (Table 3).

Changes in food eaten following sucker removal were evident in the two size-groups of walleye for which comparable data were obtained (Table 3) and coincident with changes in yellow perch abundance and feeding habits (Fig. 2). There was an eightfold increase in micro-crustaceans consumed and a twofold increase in chironomid larvae by young walleye. These changes were in the same direction noted for both young and juvenile perch. The increase in crustaceans may be related to the decreased use by adult perch of this organism, while the increased use of chironomids may be more directly related to the reduced number of suckers.

The mean volume of fish consumed by young walleye (Table 3) also increased; the consumption of minnows and darters was 68% higher in 1967 and 1970, following sucker removal than in the preremoval period. This may be related in part to reduced consumption of minnows and darters by larger walleye after sucker removal. The increased abundance of young perch in the postremoval years was not reflected in the diet of young walleye since most

TABLE 3. Food of three sizes of yellow perch and two sizes of walleye before and after sucker removal expressed as mean volume (ml) per fish and percents of total volume for each food item, Wilson Lake 1964–65 (A) and 1967 and 1970 (B).

Food Item	Yellow Perch												Walleye							
	Young-of-year				51–127 mm				> 127 mm				Young-of-year				> 229 mm			
	A (172)[a]		B (192)		A (360)		B (50)		A (285)		B (120)		A (118)		B (975)		A (390)		B (230)	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
Crustacea	0.009	63.8	0.012	74.3	0.061	43.1	0.083	66.5	0.129	35.6	0.012	3.7	0.002	3.3	0.016	14.3	tr	tr	0.04	2.1
Insecta	0.005	32.7	0.004	23.1	0.073	51.9	0.042	33.5	0.110	30.3	0.237	74.1	0.008	16.2	0.018	16.2	1.06	27.6	0.83	44.4
Diptera	tr	2.1	0.002	15.3	0.008	5.4	0.010	8.0	0.017	4.8	tr	0.2	0.008	15.9	0.015	12.9	0.01	0.3	0.03	1.5
Ephemeroptera	tr	1.7	0.001	7.0	0.059	42.0	0.024	19.4	0.071	19.7	0.185	57.8	—	—	—	—	1.02	26.5	0.76	40.9
Other[b]		28.9	0.001	0.9	0.006	4.5	0.008	6.1	0.022	5.6	0.052	16.1	—	0.3	—	3.3	—	0.8	—	2.0
Fish	tr	3.5	—	—	—	0.1	—	—	0.056	15.6	0.038	11.8	0.040	80.5	0.077	69.5	2.71	70.7	0.77	41.4
Young perch	—	—	—	—	—	—	—	—	—	—	—	—	tr	0.4	0.003	2.6	0.15	3.9	0.33	17.7
1+ perch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.99	51.9	0.05	2.9
Minnows & darters	—	—	—	—	—	—	—	—	—	—	—	—	0.025	50.5	0.042	37.8	0.57	14.9	0.39	20.8
Unidentified	—	3.5	—	—	—	—	—	—	—	—	—	—	0.015	29.6	—	29.1	—	—	—	—
Other	—	—	tr	2.6	0.007	4.9	tr	tr	0.067	18.5	0.033	10.8	—	—	—	—	0.07	1.7	0.23	12.1
Mean	0.014		0.016		0.141		0.125		0.362		0.320		0.050		0.110		3.84		1.87	

[a] Number of fish.

[b] Small amounts of Odonata, Trichoptera, Hemiptera, Coleoptera, Plecoptera, and Megaloptera.

of these perch were too large to serve as prey. No evidence of cannibalism by walleye, as reported by Forney (1974) in Oneida Lake, was observed in Wilson Lake.

The consumption of young perch by walleye 229 mm and larger increased more than twofold after sucker removal, reflecting the greater abundance of perch. The mean volume of burrowing mayfly nymphs consumed per fish decreased but their percentage in the diet increased from 26.5 to 40.9% (Table 3). Although consumption per fish was less, the larger population of younger, smaller walleye may have consumed a greater biomass of mayfly nymphs than the less abundant population of mature walleye present before sucker removal.

Though the walleye and northern pike were the principal piscivores in the lake and perch were the primary prey fish for both species, the northern pike population was small and pike tended to select larger yellow perch than did walleye.

Foods eaten by northern pike were qualitatively similar before and after sucker removal with fish comprising 99% of the diet. Young perch were not used for food in either period but perch age 1 plus made up 52.4 and 45.2% of the diet before (1964–65) and after (1967, 1970) removal, respectively. Walleye age 1 plus made up a large part of the diet in both sampling periods, but after removal a pronounced increased use of young walleye was also noted; the volume of walleye consumed was half that of perch before removal but greater than that of perch after removal (Unpublished data, Section of Fisheries Minn. Dep. Nat. Res.). The greater consumption after sucker removal may have indicated greater availability and reflected increased survival of walleye after sucker removal.

INVERTEBRATES

No persistent changes in abundance of benthic organisms of zooplankton were noted following sucker removal. Burrowing mayfly larvae, the most common invertebrates in walleye, sucker, and perch diets and chironomids were significantly less abundant in 1968 (*t*-test, $P < 0.05$) but recovered to levels that did not differ significantly from those for the preremoval period. Amphipods abundance did not change significantly. The decrease in invertebrate abundance in 1968 could not be correlated with yearly temperature regimes or with changes in the fish population or their feeding habits (Johnson 1975).

There was marked variation in zooplankton abundance between and within years and no relation between abundance and sucker removal was detected. Peaks of abundance generally occurred in mid-to-late June (Johnson 1975).

COMMUNITY STRUCTURE

White sucker — The removal of adult white suckers caused marked changes in the sucker population. Seine catches of young in 1966 and 1967 were less than 10% of the baseline catch of the 2 preremoval yr. In subsequent years, reproduction fluctuated irregularly. Only the 1973 year-class exceeded the baseline catch (Table 4).

The abundance of immature suckers (<356 mm) as measured by fall gillnet catches was low in the years prior to removal but increased after removal (Fig. 3). In 1972, gillnet catches were more than eight times the preremoval level. By 1973 substantial numbers of these fish were mature and the catch of immature declined. The growth rates of immature suckers (ages I–IV) was faster after than before removal, but significantly so for only age III fish (*t*-test, $P < 0.05$) (Johnson 1975).

The abundance of adult white sucker was severely reduced by removal and recovery by recruitment was not evident until 1972 (Fig. 3). The fall gillnet catch of 1973 was higher than before removal, but was probably biased upward by the size structure of the adult population which had a much larger proportion of small adults that were more vulnerable to the mesh sizes of the gill nets used than were the larger and older adult suckers present before removal. Spring population estimates indicated that the standing crop of adult white suckers in 1973 had recovered to only 21.2% of the estimated 40 kg/ha present at time of removal in 1966 (Johnson 1975). Recruitment of the abundant immature suckers present in 1971–73 continued and will likely restore the adult population to higher levels.

Yellow perch — Yellow perch appeared to respond sooner, and to a greater degree, than any other species to sucker removal. Abundance increased in gillnet samples and in the angler catch, and growth and condition (*K*) increased.

The abundance of young yellow perch was below that for the 1964–65 base period in 1966–67 but a strong year-class was produced in 1968, 2 yr after sucker removal. Numbers of young perch were near or above the baseline catch in most of the succeeding years. The greatest abundance was reached in 1971 at 10 times the baseline catch (Table 4).

Recruitment of these strong perch year-classes as age I plus fish was evident in fall gillnet sam-

TABLE 4. Relative abundances (percentages of mean N/ha in 1964–65) of principal small fishes caught by shoreline seining after sucker removal, Wilson Lake 1966–73.

Species	Mean N/ha 1964–65	1966[b]	1967	1968	1969	1970	1971	1972	1973
W. sucker[a]	211	9.5	1.4	0.5	75.8	0.0	30.3	12.8	156.9
Y. perch[a]	154	13.7	23.4	198.0	43.6	166.1	1516.6	152.4	87.9
Walleye[a]	22	72.7	40.9	0.0	13.6	27.3	86.4	54.5	31.8
Minnows	1,184	60.7	53.7	103.1	20.5	34.0	19.4	44.0	16.4
Darters	152	67.3	27.7	53.5	48.8	85.8	89.1	145.9	108.2

[a] Young-of-the-year.
[b] Year of sucker removal.

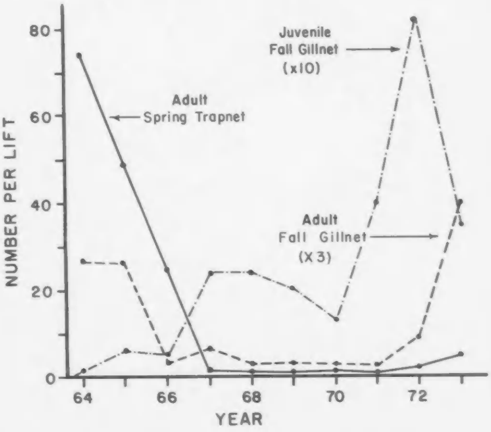

FIG. 3. Numbers of juvenile (<356 mm) and adult white sucker per fall gillnet lift, and numbers of adult white sucker per spring trapnet lift, Wilson Lake 1964–73.

pling (Fig. 4). The average gillnet catch of yellow perch the 2 yr prior to sucker removal was 1.0/lift. After removal, greater catch/lift was observed, reaching a high of 16.8/lift in 1973 and averaging 6.8 for all years after removal.

The growth rate of yellow perch increased markedly following removal of suckers. The mean annual increment of both male and female yellow perch caught in gill nets was 10 mm greater from age I to age II and from age II to age III for years following sucker removal. Females averaged about 40 mm larger at ages V and VI. However, there is some evidence that the growth of perch began to decline as their abundance increased (Johnson 1975).

The condition factor (*K*) was also higher following sucker removal. The mean condition for all sizes was 1.06 before sucker removal. It increased to 1.24 in 1967 and then declined to 1.16 in 1970 (Unpublished data, Section of Fisheries, Minn. Dep. Nat. Res.). The increase in condition factor following sucker reduction suggests that food availability increased and was highest in the years immediately following removal but declined as perch became more abundant.

Yellow perch were not recorded in the creel census before sucker removal. The largest harvest of perch was in 1972 when 0.2 kg/ha were taken (Johnson 1975). The presence of yellow perch in the sport fishing catch in the later years reflected the increased abundance of this species.

Walleye — The response of walleye to sucker removal was not as pronounced as that of yellow perch, but data for the last 2 yr of the study suggest that it may be similar. Fall gillnet abundance indices (Fig. 4), population estimates, and angler harvest of walleye (Table 5) all indicated a larger walleye population during the last 2 yr of study, although abundance of young walleye, as measured by shoreline seining, was lower than

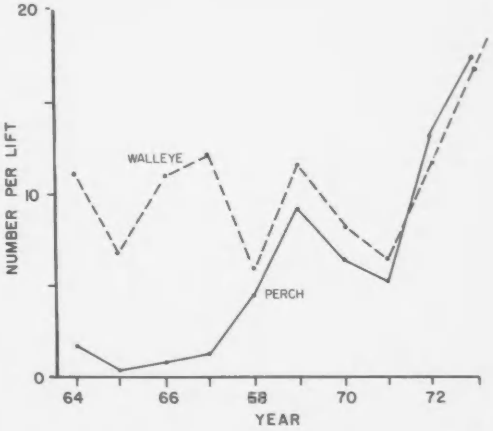

FIG. 4. Relative abundances of age I plus yellow perch and walleye as indicated by numbers per fall gillnet lift, Wilson Lake 1964–73.

TABLE 5. Walleye sportfishing harvest statistics before and after sucker removal, Wilson Lake 1964–73.[a]

	1964	1965	1967	1969	1970	1971	1972	1973
Number	1676	1031	1266	1344	2216	2593	3371	4524
Kilograms	876.6	579.2	496.9	527.9	850.5	1089.0	1189.5	1634.4
Av. wt. (kg)	0.52	0.57	0.41	0.41	0.36	0.41	0.36	0.36
Yield (kg/ha)	3.6	2.4	2.0	2.1	3.5	4.5	4.9	6.7
N/man-hour	0.29	0.24	0.29	0.32	0.30	0.28	0.35	0.40
Exploitation rate, adult stock	—	0.170	—	0.163	0.153	0.218	0.174	0.183

[a] Sucker removal, 1966.

the 1964–65 baseline value in the years following sucker removal (Table 4). The slower response of walleye may have been due in part to dependence on an expanding perch population.

The catch per fall gillnet lift in the pre- and immediate postremoval years (Fig. 4), fell within the same range as that found in similar lakes in the area with walleye–sucker populations. The mean catch/lift of walleye for 28 similar lakes in the same county as Wilson Lake, surveyed during 1961–66, was 7.20 (SD = 4.36). The mean catch from 21 of these lakes was within one standard deviation of the series mean. The mean catch/lift of walleye in Wilson Lake in 1973 exceeded the series mean by more than two standard deviations (Unpublished data, Section of Fisheries, Minn. Dep. Nat. Res.).

The number of walleye larger than 305 mm, estimated in the spring of 1965 and each year from 1969 through 1973, increased in 1972 and 1973. The Petersen type estimates for the populations with 95% confidence limits, mean weight (kg) and standing crop (kg/ha) were:

Year	Population	Mean weight	Standing crop
1965	5986 ± 2651	0.64	15.5
1969	3434 ± 1094	0.50	7.0
1970	6389 ± 2071	0.64	16.5
1971	6205 ± 1769	0.50	12.6
1972	9087 ± 2594	0.54	20.2
1973	8856 ± 1988	0.59	21.3

The 1972 and 1973 estimates were 60% higher than previous levels and the standing crop was 34% higher.

The growth rate of walleye was slower than for other waters in Minnesota (Dobie 1970), but was nearly typical of lakes in the Precambrian shield (Unpublished data, Section of Fisheries, Minn. Dep. Nat. Res.). All sizes grew faster in the years following sucker removal through 1971 except in 1968; reduced growth in 1968 may have been related to the decrease in the invertebrate population. In 1972–73 there was a sharp decline in growth for all size-groups, in association with the increase in population size in those years (Johnson 1975). Whether this reduced growth rate persisted in later years is unknown.

The condition of male walleye less than 460 mm was similar in 1969 to those of the same size before sucker removal, but declined annually from 1970 to 1973. Male walleye 460 mm or larger were in better condition (*K* 0.91) after removal (1969 to 1972) than the same size-group before sucker removal (*K* 0.87), but in 1973 condition of these fish declined to about preremoval levels (*K* 0.86), (Johnson 1975). This decline in condition may reflect the greater abundance of walleye in recent years.

The mean annual harvest of walleye by the sport fishery before sucker removal was 3.0 kg/ha (Table 5). From 1970 through 1973 the annual walleye harvest increased each year reaching 6.7 kg/ha in 1973 and averaged 4.9 kg/ha for the 4-yr period. The mean annual harvest of walleye alone in these years exceeded the predicted total fish yield (2.7 kg/ha) by 81.5% on the basis of the morphoedaphic index (Ryder 1965) of 4.8.

Much of the increased harvest of walleye in recent years consisted of fish recruited within the season. In 1965, fish recruited during the season comprised 26.5% of the harvest. The numbers of walleye 305 mm or larger in the spring, harvested from 1969 to 1973, reflect changes in abundance evident from the population estimates. The harvest of these fish was 59% greater in 1973 than in 1965. Walleye below this size increased nearly eightfold from 1965 to 1973 and comprised 52.0–64.2% of the harvest in the last 5 yr, 1969–73, of the study (Johnson 1975).

Before sucker removal, the harvest was mainly of fish of age-classes V–VII; after sucker removal, mainly of walleye from age-classes III–V. In 1972 the modal group was age-class II, the strong 1970 year-class; in 1973, this year-class contributed an estimated 61.3% of the harvest (Fig. 5).

No trend in the exploitation rate of the adult stock corresponding to the increased fishing pressure was evident (Table 5). The mean rate of

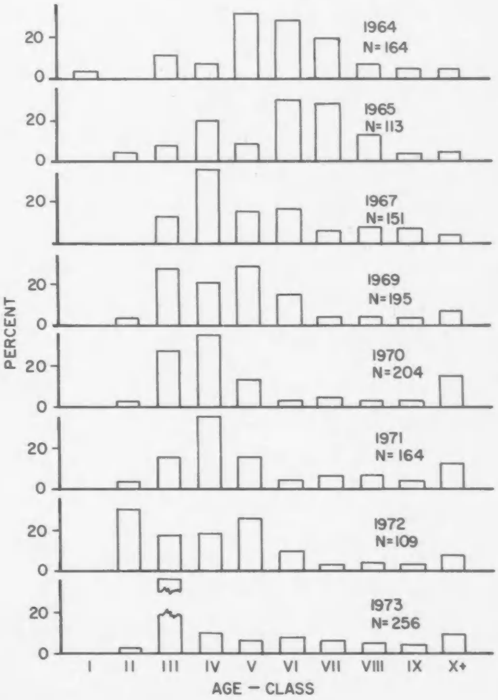

FIG. 5. Age compositions of walleye in the sport-fishing catches, Wilson Lake 1964–73, (not censused 1966 and 1968).

exploitation for the 6 yr was 0.175. This tends to support other evidence that the increased walleye yield was due mainly to recruitment of strong year-classes produced after sucker removal.

The annual mortality rate for the adult population was estimated to be 0.378; annual expectation of death from natural causes was estimated to be 0.203 (Johnson 1975). Since natural mortality exceeded fishing mortality, it appears that adult walleye in Wilson Lake could have sustained a higher rate of fishing in the years before and immediately following sucker removal.

Northern pike — The reduction of the sucker population appeared to have little effect on the northern pike population. The catch per fall gill-net lift varied between 0.5 and 2.0 during the period of study and no trends were evident (Johnson 1975).

Prey species — Minnow abundance, as measured by shoreline seining, was substantially lower in most years after than before sucker removal (Table 4). Darters appeared to be less abundant from 1966 through 1971, but in 1972 and 1973 were caught in greater numbers than before sucker removal. The mean volume of minnows and darters consumed by young walleye increased but declined for larger walleye and all sizes of yellow perch. The greatest abundance of walleye and perch in recent years probably subjects minnows and darters to greater predation.

General Discussion

Evaluation of the effect of sucker removal on the walleye population was confounded by an increase in fishing pressure and harvest which was coincidental with the improvement of the access road and the publicity about the good fishing in a magazine with national distribution in 1971. Also, the large year-classes in 1966, the year of sucker removal, and in 1970 were produced in years when walleye reproduction was generally good throughout major walleye lakes in Minnesota.

Nevertheless, there were indications that the removal of suckers ultimately benefited walleye. The switch of adult perch from a diet with a large proportion of crustaceans and small insects to other food was accompanied by greater use of these smaller organisms by young walleye and smaller perch. Young perch were too large to be eaten by young walleye, but became more common in stomachs of large walleye. Coincidentally, consumption of smaller prey fishes decreased. These may have been used by young walleye. The increased abundance of young perch may also have enhanced survival of juvenile walleye.

The increased harvest of walleye was a desirable result but probably cannot be sustained. The excess of actual yield over predicted yield suggests that the Wilson Lake walleye population may have been overexploited in recent years. There was no apparent change in the rate of exploitation of adult walleye, but the high yield in recent years was dependent mainly on one or two strong year-classes harvested at relatively small sizes.

The large, mature stock of suckers apparently suppressed survival and recruitment of its own progeny but the mechanism of suppression is a matter of conjecture. Abundance of young suckers on shoal areas was low until 1973, but survival after the first year appeared to be relatively high after removal of the adults. Catches in sampling gill nets indicated a rapidly growing sucker population 5–7 yr after sucker removal, suggesting that the adult sucker population may, in time, reach former levels and revert to a stable stock of fish.

White sucker removal may benefit percids in the relatively infertile lakes of northeastern Minnesota, where the number of species present is low. In more productive waters with a more diversified species composition, the productivity released by removing white suckers might be assimilated by other species that feed at the same tropic level with no measurable response by percid populations.

The complex feeding interrelations of competing species provides some insight on the direction and extent of changes that can occur when the abundance of one species is reduced. It also indicates that both interspecific and intraspecific interactions must be measured to fully understand even relatively simple ecosytsems.

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Food Consumption of Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*) in Relation to Food Availability and Physical Conditions in Lake of the Woods, Minnesota, Shagawa Lake, and Western Lake Superior[1,2]

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SWENSON, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643–1654.

Measurement of walleye (*Stizostedion vitreum vitreum*) daily food consumption rates and prey density in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior showed a general relationship exists between the two variables. Daily food consumption increased from 1 to 3% of body weight at prey densities up to 400 mg · m^{-3}. Abundance of age 0 yellow perch (*Perca flavescens*) in Lake of the Woods, Minnesota, and Shagawa Lake resulted in much higher prey densities and daily food consumption to 4% of body weight. In Lake Superior where walleye fed exclusively on rainbow smelt (*Osmerus mordax*), prey density did not exceed 300 mg · m^{-3} and daily food consumption averaged less than 2.5% of body weight.

Hourly food consumption by walleye changed in response to variation in prey availability and light intensity. Night feeding predominated during July and August when walleye fed on pelagic age 0 yellow perch. Feeding appeared to be continuous or crepuscular during June and September when larger demersal prey fish or invertebrates were eaten. Food consumption declined when prey concentrated near aquatic macrophytes and under conditions of high light intensity. Walleye daily food consumption was not influenced by a change in temperature from 20 to 15°C.

Daily food consumption of Lake of the Woods, Minnesota sauger (*Stizostedion canadense*) averaged less than walleye and was influenced by wave activity and prey density. Demersal prey was utilized by sauger throughout the 24 h-day.

Key words: Percidae, food consumption, behavior, feeding, walleye, *Stizostedion vitreum vitreum*, sauger, *S. canadense*, light

SWENSON, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643–1654.

La mesure des taux de consommation quotidienne de nourriture et de densité des proies du doré jaune (*Stizostedion vitreum vitreum*) dans le lac des Bois, Minnesota, le lac Shagawa et le lac Supérieur occidental démontre qu'il existe une relation générale entre ces deux variables. La consommation quotidienne de nourriture augmente de 1 à 3% du poids corporel à des densités de proies allant jusqu'à 400 mg · m^{-3}. L'abondance des perchaudes (*Perca flavescens*) d'âge 0 dans le lac des Bois, Minnesota, et le lac Shagawa a pour résultat des densités de proies beaucoup plus élevées et une consommation quotidienne de nourriture allant jusqu'à 4% du poids corporel. Dans le lac Supérieur, où le doré jaune se nourrit exclusivement d'éperlans arc-en-ciel (*Osmerus mordax*), la densité des proies n'excède pas 300 mg · m^{-3}, et la consommation quotidienne de nourriture est en moyenne inférieure à 2.5% du poids corporel.

La consommation horaire de nourriture par le doré jaune change en réponse à la variation

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Contribution No. 15, Center for Lake Superior Environmental Studies, University of Wisconsin-Superior, Superior, Wis. 54880, USA.

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dans l'accessibilité des proies et l'intensité lumineuse. L'alimentation nocturne prédomine en juillet et août, alors que le doré jaune se nourrit de perchaudes pélagiques d'âge 0. L'alimentation semble être continue ou crépusculaire en juin et septembre, alors que le doré se nourrit de proies démersales plus grandes, poissons ou invertébrés. La consommation de nourriture diminue quand les proies se concentrent à proximité des macrophytes aquatiques et dans des conditions de forte intensité lumineuse. La consommation quotidienne de nourriture par le doré jaune n'est pas affectée par un changement de température de 20 à 15°C.

La consommation quotidienne de nourriture par le doré noir (*Stizostedion canadense*) du lac des Bois, Minnesota, est en moyenne moindre que celle du doré jaune et est affectée par l'action des vagues et la densité des proies. Le doré noir mange des proies démersales tout au long de la journée de 24 h.

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INFORMATION on the feeding behavior of walleye (*Stizostedion vitreum vitreum*) and sauger (*Stizostedion canadense*) is important to our understanding of percid communities and to effective management of these resources. In this investigation estimates of daily and hourly food consumption rates are related to species composition of prey populations, prey density, prey distribution, prey size, utilization of cover by prey, surface light intensity, temperature, and wave activity to measure the influence of these factors on walleye and sauger feeding success and feeding time.

Studies were conducted on Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. Differences in food and physical habitat conditions between the three waters were important to measuring effects on feeding. Swenson and Smith (1976) showed that Lake of the Woods, Minnesota, prey populations are dominated by age 0 yellow perch and prey densities vary between approximately 60–800 $mg \cdot m^{-3}$. Shagawa Lake possesses a comparative similar prey species complex but densities reach much higher levels due to cultural enrichment. Western Lake Superior fish populations are dominated by rainbow smelt (*Osmerus mordax*) occurring at relatively low densities. Erosion of red-clay sediments in western Lake Superior reduces water clarity and light penetration during and after storm winds. Variation in western Lake Superior (Table 1) between the three lakes and diurnal changes provided an opportunity to measure the influence of light penetration on walleye feeding behavior. Large size and regular shoreline of Lake Superior and Lake of the Woods resulted in storm waves and curtailed development of aquatic vegetation which was prevalent in the protected bays of Shagawa Lake (Table 1).

Swenson and Smith (1976) failed to identify differences in daily food consumption of Lake of the Woods walleye at temperatures of 14 and 20°C. Samples collected over the same temperature range from Shagawa Lake provided improved precision in measuring the influence of temperature on walleye feeding in this study.

Materials and Methods

Walleye, sauger, and prey fish were collected with a semiballoon trawl, 7.6-m headrope and 2-cm bar mesh with a 0.6-cm bar mesh cod liner. Standard hauls filtered and estimated 3460 m^3 of water in 10 min on Lake Superior, 2600 m^3 in 7 min on Lake of the Woods and 1608 m^3 in 5 min on Shagawa Lake. A smaller trawl with a 5-m headrope and 0.64-cm bar mesh was used on the bottom and at midwater depths to sample prey populations in Lake Superior because age 0 rainbow smelt escaped through the mesh of the larger gear. Standard 10 min hauls filtered approximately 1950 m^3 of water. Trawling speed was maintained at 4.8–5.7 $km \cdot h^{-1}$ (3.0–3.5 $mi \cdot h^{-1}$). Use of trawl catches in defining and comparing prey and predator densities in the three waters was based on the assumption that variation in trawling speed and distance did not influence catchability of prey or predators. Comparison of length–frequency distributions for trawl and gillnet catches from Lake of the Woods suggested that some walleye and sauger exceeding 400 mm TL escaped capture by the trawl (Swenson and Smith 1976). Trawl avoidance by larger walleye probably occurred on Shagawa Lake and Lake Superior as well.

The number of age 0 and older fish captured was recorded for each species. Lengths and weights were taken for walleye and sauger used in the feeding analyses, and representative samples from prey populations. Prey density was estimated from trawl catches as weight of prey per volume of water sampled ($g \cdot m^{-3}$). Trawl catches did not provide an adequate estimate of prey densities during July for Shagawa Lake and from July 1 to mid-August for Lake of the Woods. During these periods pelagic behavior and small size significantly reduced catches of age 0 yellow perch, the dominant prey species in both lakes. Decline in catch demonstrated vulnerability stabilized when age 0 yellow perch reached approximately 40 mm, the approximate size at which Kelso and Ward (1976) and Ney and Smith (1976) found perch become demersal. A minimum estimate of prey density for sampling days occurring during

TABLE 1. Physical data for the three waters studied.

Characteristic	Lake of the Woods, Minnesota	Shagawa Lake	Western Lake Superior Turbid Zone (8.5 ppm)	Western Lake Superior Clear Zone (0.5 ppm)
Latitude	49°00′	47°55′	46°46′	
Longitude	95°00′	91°52′	92°02′	
Surface area (ha)	122,000	925	—	
Depth (m)				
maximum	12	13	12[e]	
mean	7.3	6.7	6[e]	
Temperature range June–September (°C)	11–21	14–23	7–19	5–17
Vegetation (macrophytes)	Sparse, mainly emergent	Dense at 1–3 m in bays	None	None
Light penetration (Depth m, of 1% surface light)	2.2 (July–Sept. 1969)	3.5 (July 1974–75)[b]	2	15
Turbidity	6.5–49 JTU[a]	—	122–10ppm[d]	0–10[d]
pH	7.3[a]	7.2[b]	7.5[d]	7.4[d]
Total alkalinity (ppm)	67[a]	22[c]	40[d]	43[d]
Conductivity (μ ohms)	115[a]	60[c]	101[d]	97[d]
Total phosphorus (ppm)	0.060[a]	0.031[b]	0.067[d]	0.036[d]

[a] National Biocentrics Inc. (1973).

[b] Personal Communication: Paul Smith, Environmental Protection Agency, Shagawa Lake Restoration Project, Ely, Minn.

[c] Larson et al. (1975).

[d] Bahnick (1975).

[e] Maximum at which walleye were captured and mean sampling depth for Western Lake Superior sampling program. Depths given for other waters are lake maximum and means.

the period of changing vulnerability was defined as the sum of the average number of age 0 yellow perch caught during the first 2 sampling days after perch length averaged 40 mm and the calculated consumption of yellow perch by walleye and sauger captured in a standard trawl haul for all days during the intervening period. Catches of other prey species were added to the estimated yellow perch densities in estimating total prey densities.

Water temperature and depth were measured with each trawl on Lake of the Woods and Shagawa Lake, and trawl distance was measured on selected days. On Lake Superior, temperature[3] and transmissometer[4] probes were towed close to the bottom in a Tri-Vane (Swenson unpublished data) which also metered haul distances. Total suspended solid concentration (ppm) was estimated from the relationship between percentage light transmittance and galimetric measurements of total suspended solids (APHA et al. 1971). At Shagawa Lake, surface light was monitored with a radiometer within 3 km of the lake by the U.S. Environmental Protection Agency. An index of light intensity for Lake of the Woods was developed from cloud cover data collected at Kenora, Ontario, by the Canadian Ministry of Atmosphere and Environmental Services. Wind directions and wave heights were estimated during Lake of the Woods sampling. Waves were rated on a scale of 0–4 with a rating of 0 approximating calm conditions and 4 equivalent to a 1 m trough to crest average wave height.

Estimation of daily food consumption by walleye and sauger was based on analysis of stomach content from field collections and laboratory estimates of gastric digestion rates (Swenson and Smith 1973). Stomachs from 2028 Lake of the Woods walleye and sauger collected during 27 days, June–September 1969 and 1970 (Swenson and Smith 1976), 840 Shagawa Lake walleye collected on 17 days, June–September 1974 and 1975, and 88 Lake Superior walleye collected during 5 days, July–September 1973 were analyzed to estimate daily and hourly food consumption rates. It was necessary to subsample from a total of 354 walleye stomachs from Lake Superior to meet the conditions included in the laboratory digestion studies of Swenson and Smith (1973) upon which estimates of food consumption are based. Digestion data were not applicable for most samples collected on 22 days during June–September 1973 because sizes of fish captured, sizes of food eaten, or lake temperatures were not included in the digestion studies. The total sample was used to define Lake Superior walleye diet and effects of suspended solids on feeding.

Electivity indices (Ivlev 1961) were calculated from the percentage of each prey species in the daily meal and percentages in trawl catches for Lake of the Woods and Shagawa Lake. Lake of the Woods calculations were based on estimates of daily food

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[3] Yellowsprings Instrument Co. Model 43TD telethermometer, Yellow Springs, Ohio.

[4] Hydroproducts, Inc. Model 410Br transmissometer, Box 2528, San Diego, Calif.

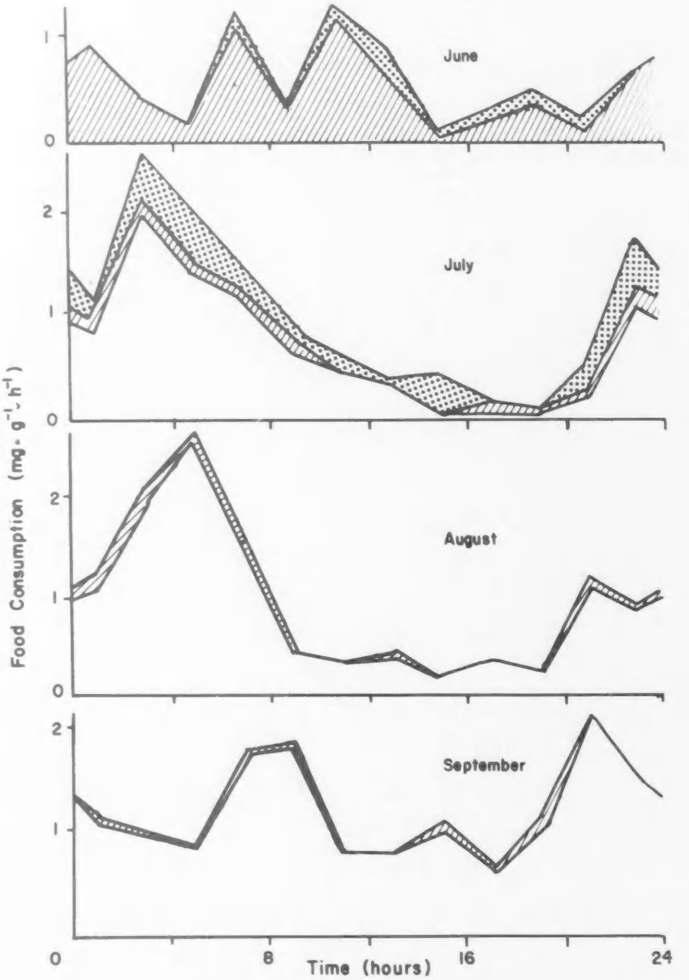

FIG. 1. Hourly food consumption ($mg \cdot g^{-1} \cdot h^{-1}$) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Lake of the Woods walleye.

consumption and prey density presented by Swenson and Smith (1976). Although biased by trawl selectivity, electivity indices were useful in identifying changes in feeding associated with variation in prey availability.

Factors Influencing Walleye Feeding

Food quality — Invertebrates and fish were eaten primarily during night and twilight hours in both Lake of the Woods and Shagawa Lake (Fig. 1 and 2). Lake of the Woods walleye over 200 mm TL ate an average of 2.5 and 5.6 $mg \cdot g^{-1} \cdot day^{-1}$ of invertebrates, mainly the mayfly *Hexagenia limbata* during June and July, respectively (Table 2). Chironomidae and mayflies were the most common invertebrate items in Shagawa Lake walleye daily meals.

Daily food consumption of walleye was influenced by abundance and location of yellow perch. In Shagawa Lake average daily food consumption for June was highest during 1975 (Table 2) when yearling yellow perch abundance was high (Table 3). In 1974 although June consumption of invertebrates and other prey fish species was high, abundance of yearling perch (Table 3) and total daily food consumption ($mg \cdot g^{-1} \cdot day^{-1}$)

TABLE 2. Total daily food consumption (g·individual^{-1} and mg·g^{-1}) and daily consumption of major forms (numbers of prey consumed daily 100 m^{-3}) by walleye over 200 mm TL in Shagawa Lake, 1974 and 1975 and western Lake Superior, 1973. Comparable data for Lake of the Woods, Minnesota, were given by Swenson and Smith (1976). Values in parenthesis are percentages of the meal.

Month	Sample size (No.)	Mean wt. (g)	Total g·ind^{-1}	Total mg·g^{-1}	*Perca flavescens*	*Percopsis o.*	*Osmerus mordax*	*Notropis hudsonius*	Other Fish	Invert.
Shagawa Lake										
1974										
June	131	105	1.6	15.0	0(0)	0(3)	—	0.36(30)	(19)	(49)
July	80	145	5.6	38.9	12.10(96)	0(0)	—	0.17(2)	(>1)	(2)
Aug.	111	98	3.1	32.2	1.22(75)	0(0)	—	0.15(9)	(3)	(14)
Sept.	23	135	3.5	26.1	0.96(57)	0(0)	—	0.83(38)	(0)	(4)
1975										
June	101	280	3.4	24.5	0.45(56)	0.02(3)	—	0(0)	(10)	(31)
July	140	177	6.6	39.5	11.94(90)	0(0)	—	0.07(1)	(2)	(6)
Aug.	78	180	6.2	34.3	1.13(88)	0.01(2)	—	0.50(3)	(6)	(>1)
Early Sept.	85	252	7.8	31.0	0.61(69)	0.03(2)	—	0.05(5)	(18)	(7)
Late Sept.	91	265	3.5	13.7	0.16(83)	0(0)	—	0.02(5)	(9)	(4)
Western Lake Superior										
1973										
July	35	129	3.1	22.8	—	—	0.5(100)	—	—	—
Aug.	31	240	5.1	19.5	—	—	0.6(100)	—	—	—
Sept.	22	148	3.1	21.0	—	—	1.0(100)	—	—	—

TABLE 3. Densities of principal walleye and sauger prey (number 100·m^{-3}) and of total prey (mg·m^{-3}) in the three waters studied. Values in parentheses are for depths greater than 5 m.

Month	Days sampled	Net lifts	*Perca flavescens* Age 0	*Osmerus mordax*	*Percopsis omiscomaycus* Age 0+	*Notropis* sp. Age 0+	Total prey density
Lake of the Woods, Minnesota (1969–70)[a]							
June	15	144(16)	0.1(0.0)	—	2.3(15.8)	0.2(0.0)	100(576)
July	9	106(11)	86 (3.0)[c]	—	3.3(13.5)	0.2(0.1)	374(486)[c]
Aug.	17	128(27)	29.6(5.2)	—	5.6(24.6)	0.9(0.0)	532(698)
Sept.	9	87(20)	21.6(10.9)	—	7.3(30.6)	0.7(0.0)	616(1008)
Shagawa Lake, Minnesota (1974–75)							
June 1974[b]	2	14(2)	0.0(0.0)	—	4.0(2.7)	2.4(0.2)	132(68)
June 1975[b]	3	20(16)	19.5(0.8)	—	0.3(0.9)	0.7(0.1)	585(40)
July	4	19(21)	500 (23.6)[c]	—	2.7(8.0)	1.5(1.8)	2528(388)[c]
Aug.	4	15(9)	84.7(10.1)	—	16.4(8.0)	14.3(1.1)	2691(439)
Sept.	5	26(17)	24.3(9.7)	—	8.8(6.8)	5.5(4.3)	1715(871)
Oct.	1	6(3)	66.9(1.7)	—	0.5(0.4)	5.5(1.5)	2127(150)
Nov.	1	4(2)	1.8(0.9)	—	0.1(4.7)	0.4(0.1)	117(314)
Western Lake Superior (1973)							
June	4	6	—	7.4	0.2	—	282
July	4	6	—	8.3	0.3	—	157
Aug.	4	6	—	52.2	0.3	0.2	169
Sept.	4	6	—	46.5	1.6	0.2	317

[a] Information for Lake of the Woods, Minnesota, was converted from Swenson and Smith (1976).

[b] Estimates given separately for the 2 years to illustrate major differences in abundance of yearling yellow perch.

[c] Estimates for water under 5 m are corrected for incomplete vulnerability of age 0 yellow perch to the trawl by procedures described in "Methods."

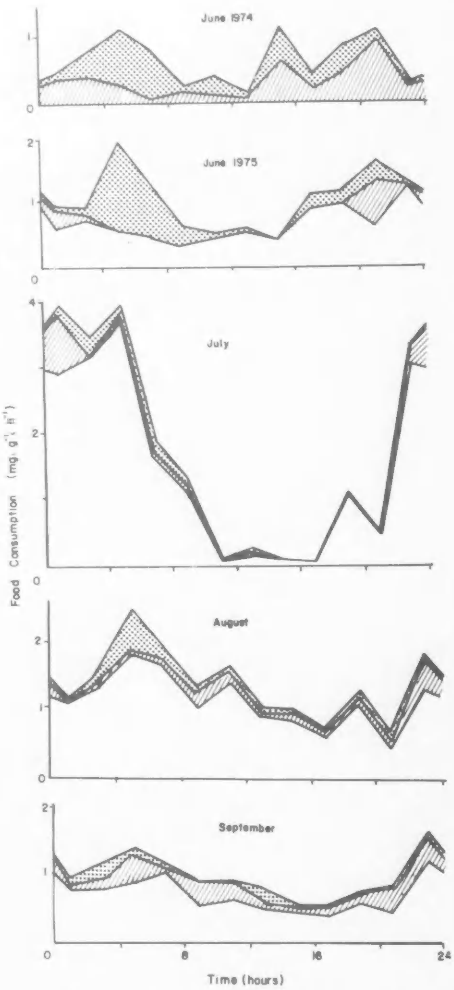

FIG. 2. Hourly food consumption (mg·g⁻¹·h⁻¹) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Shagawa Lake walleye.

was low. June 1975 consumption averaged 24.5 $mg \cdot g^{-1} \cdot day^{-1}$ in comparison with 11.6, 7.5, and 15.0 $mg \cdot g^{-1} \cdot day^{-1}$ for 1969, 1970, and 1974, respectively. Increased abundance of age 0 yellow perch during July in both Lake of the Woods and Shagawa Lake was associated with increased walleye daily food consumption and a change to night feeding (Table 2, Fig. 1 and 2). The highest daily food consumption occurred during July in Shagawa Lake where walleye fed primarily at night and ate approximately 4% of their body weight per day (Fig. 2, Table 2). Prominence of night feeding declined during August in Shagawa Lake and during September in Lake of the Woods. The trend away from night feeding appeared related to a closer association between age 0 yellow perch and the lake bottom.

Trout-perch (*Percopsis omiscomaycus*) were the second most abundant prey in the three waters (Table 3) but were uncommon in the daily meals of walleye (Table 2; Swenson and Smith 1976). For both Lake of the Woods and Shagawa Lake electivity of trout-perch was strongly negative (Table 4) during all sampling months suggesting that trout-perch are avoided or are not available. Electivity indices for *Notropis* sp., which were common in Lake of the Woods and Shagawa Lake, were positive or zero during periods of reduced age 0 yellow perch abundance but became negative during periods of high perch abundance. Shagawa Lake walleye appeared to positively select age 0 black crappie (*Pomoxis nigromaculatus*).

Lake Superior walleye fed only on rainbow smelt, which comprised 95% by weight of the prey-sized fish in trawl catches. The data suggested that western Lake Superior walleye utilize rainbow smelt in approximate proportion to their abundance.

Prey density — Monthly averages of Lake of the Woods walleye daily food consumption estimates increased with prey densities up to 300 $mg \cdot m^{-3}$ but averaged approximately 3% of body weight at prey densities of 300–800 $mg \cdot m^{-3}$ (Swenson and Smith 1976). Daily food consumption by Shagawa Lake walleye approximated 4% of body weight during July and August, when prey densities exceeded the maximum encountered in Lake of the Woods. Observations for the three waters were combined to determine if a general relationship could be identified between monthly averages of daily food consumption and prey density. For this analysis, prey densities were estimated from trawl catches in water shallower than 5 m except during late September when prey and predator concentrated at greater depths in Shagawa Lake and data for all sampling depths was combined. Trout-perch were not included in estimates of prey density because of low utilization by walleye in all three lakes.

Daily food consumption increased with prey densities between 10 $mg \cdot m^{-3}$ and 3500 $mg \cdot m^{-3}$ with the greatest increase occurring at densities from 10 to 400 $mg \cdot m^{-3}$ (Fig. 3). Daily food consumption averaged between 3–4% of body weight over the 400–3500 mg m^3 range of prey densities. Differences between July feeding rates in Lake of the Woods and Shagawa Lake were large (Fig. 3) and resulted from major differences in

TABLE 4. Electivity indices (Ivlev 1961) of major prey consumed by walleye over 200 mm in Lake of the Woods, Minnesota, and Shagawa Lake.

Month	*Perca flavescens*	*Percopsis omiscomaycus*	*Notropis* sp.	*Pomoxis nigromaculatus*
		Lake of the Woods, Minnesota		
Walleye				
June	0.0	−0.6	+0.6	—
July	+0.2	−1.0	+0.2	—
Aug.	+0.3	−1.0	−0.1	—
Sept.	+0.2	−1.0	−0.7	—
Sauger				
June	−1.0	0.0	−0.2	—
July	−0.3	+0.4	−1.0	—
Aug.	+0.1	−0.2	−0.1	—
Sept.	−0.4	+0.2	+0.5	—
		Shagawa Lake		
Walleye				
June	0.0	−0.7	0.0	—
July	+0.3	−0.8	−0.9	+1.0
Aug.	+0.3	−0.9	−0.4	−0.6
Sept.	+0.3	−1.0	−0.2	+0.7

abundance and growth of age 0 yellow perch. In Shagawa Lake age 0 yellow perch averaged 35 mm by the middle of July, in comparison with 30 mm in Lake of the Woods. High abundance of yearling yellow perch during June 1975 also resulted in higher June consumption rates in Shagawa Lake (Fig. 3, Table 2). Low prey density in Lake Superior (Table 3) limited daily consumption to an average of approximately 2% of body weight (Fig. 3).

Physical conditions — Walleye consumption of age 0 yellow perch was greatly restricted during late September 1975 (Table 2, Fig. 3) when perch availability in open water was below 200 $\text{mg}\cdot\text{m}^{-3}$ but exceeded 1000 $\text{mg}\cdot\text{m}^{-3}$ in areas of aquatic macrophytes. Vegetation appears to reduce food availability to walleye by providing cover for some prey species which concentrate in these areas where walleye density is low. Shagawa Lake walleye catches in areas with aquatic macrophytes were low but catches on age 0 Centrarchidae were highest in these areas throughout most of the growing season.

Daily food consumption rate did not change with water temperature during periods when food abundance exceeded 400 $\text{mg}\cdot\text{m}^{-3}$ in Lake of the Woods and Shagawa Lake. Daily food consumption at 14–15.5°C (11 days during June and late September) and at 20–22°C (10 days during August and early September) averaged 30.0 and 29.1 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$, respectively. Higher stomach volumes occurred during the lower temperature periods (t-test; $P < 0.01$). Laboratory digestion studies show a positive relationship between stomach volume and food digested h^{-1} (Fig. 4). Because more food can be processed through the digestive system at higher stomach volumes, the results show that for the range of temperatures tested, limiting effects of low temperature on digestion are compensated by increased stomach volumes. By feeding throughout the day during periods of reduced temperature and high food availability, walleye maintained high stomach volumes, digestion rates, and food consumption rates.

Predominance of night and twilight feeding by Lake of the Woods and Shagawa Lake walleye indicates high light intensity may be a significant factor influencing daily food consumption. Midday feeding was greatest during June and September when walleye ate more demersal prey. Light intensity and the percentage of the total meal consumed between 08:00–18:00 CST for Shagawa Lake walleye were ranked for six periods during which a minimum of two estimates of food consumption were available for days characterized by similar prey densities. The ranks were negatively correlated ($r_s = -0.89$; $P < 0.05$) demonstrating walleye food consumption during daylight hours is limited by high light intensity. A negative but insignificant correlation was found from a similar analysis of Lake of the Woods data ($r_s = -0.15$; $P > 0.05$).

Red-clay turbidity and inshore walleye densities in Lake Superior were positively correlated ($R = 0.69$; $P < 0.01$). Light penetration is reduced by red-clay turbidity (Table 1) indicating

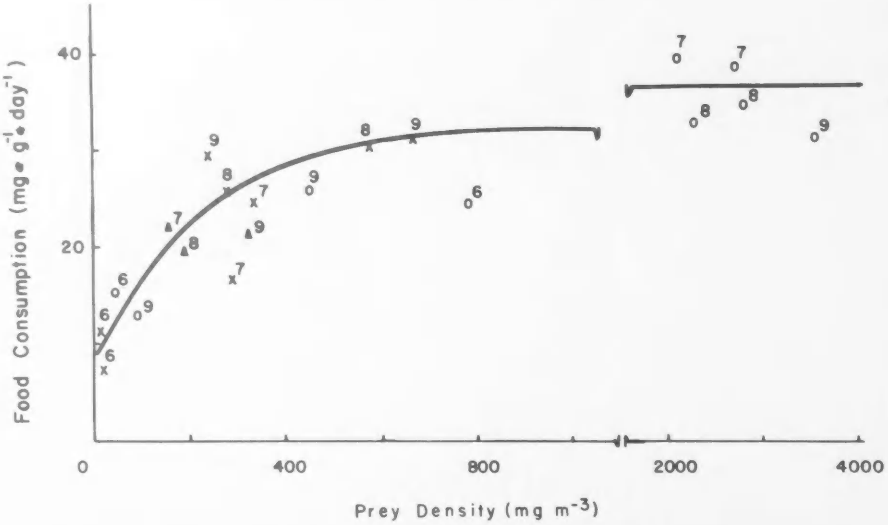

FIG. 3. Relations between monthly averages of walleye daily food consumption rates and prey densities for Shagawa Lake (○), Lake of the Woods, Minnesota (×) and western Lake Superior (▲). Numerals indicate calendar month.

the relationship to turbidity may be in response to changes in light levels. Stomach volume of Lake Superior walleye appeared to increase with turbidity but differences were not significant ($P > 0.05$).

Factors Influencing Sauger Feeding

Lake of the Woods sauger daily meals included a smaller percentage of invertebrates during June than walleye (Fig. 5) and larger quantities of trout-perch (Swenson and Smith 1976). Trout-perch comprised 85% of the food consumed by sauger during June (Swenson and Smith 1976) when midday feeding predominated (Fig. 5). Electivity indices suggested that trout-perch are eaten in approximate proportion to their relative abundance in prey fish populations (Table 4). Although percentages of age 0 yellow perch increased to 33 and 63% in July and August sauger meals, as a result of increased night active feeding on perch (Fig. 5), electivity indices continued to suggest preference or higher availability of trout-perch (Table 4).

Rank correlations suggested high light intensity associated with reduced cloud cover lowered daily food consumption of sauger during midday (08:00–18:00 CST; $r_c = -0.37$) but the relationship was not significant ($P > 0.05$).

Regression analysis showed that daily food consumption by sauger increased with wave activity on Lake of the Woods ($P < 0.01$). The association between daily food consumption and wave activity ratings could result from reduced light penetration during periods of increased wave action.

In contrast to the findings of Swenson and Smith (1976) which did not consider wave intensity, a significant relationship (Fig. 6; $P < 0.05$) between daily food consumption of Lake of the Woods sauger and prey density was observed. Variability between daily food consumption estimates was controlled by omission of data collected during days of extremely low or high wave activity (ratings 1 and 4).

Discussion

Predominance of nocturnal feeding, low percentage of trout-perch and relatively high percentages of age 0 yellow perch, rainbow smelt, and *Notropis* sp. in their daily meals showed that walleye utilize pelagic prey particularly during July and August. Pelagic behavior has been identified for smelt in turbid waters of Lake Superior (Swenson unpublished data), for age 0 yellow perch (Forney 1971; Kelso and Ward 1976) and for spottail shiners (Smith and Kramer 1964). Absence of trout-perch from midwater trawl catches in Lake Superior (Swenson unpublished data) and their food habits (Anderson and Smith 1971) indicate a close association with the

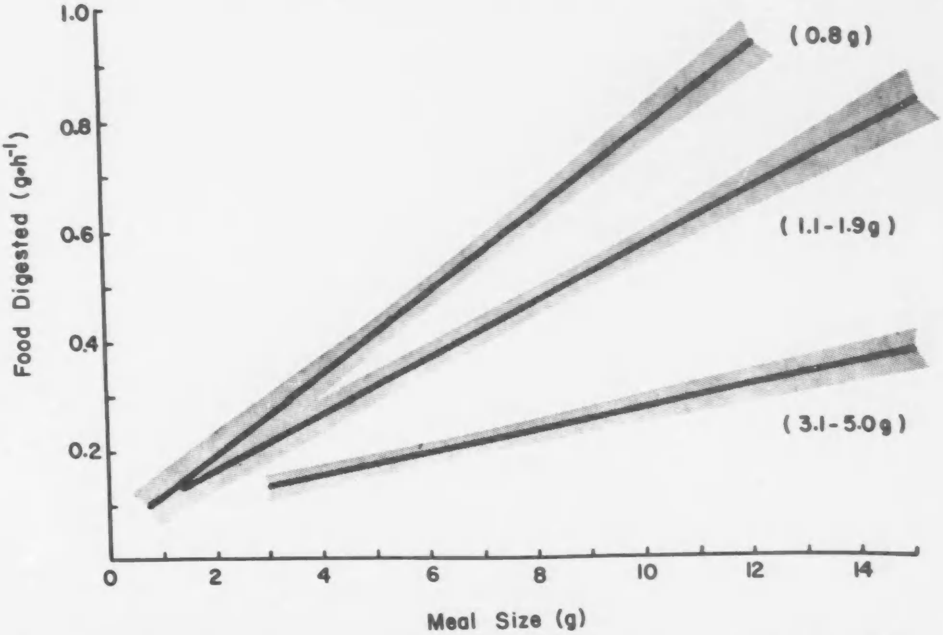

FIG. 4. Relations between walleye and sauger digestion rate and meal size in laboratory experiments including 1.1–1.9 g and 3.1–5.0 g prey at 14.5°C and 0.8 g prey at 20°C. Estimates are based on methods and 371 observations described by Swenson and Smith (1973). Shaded areas include 95% confidence limits.

bottom. Low daily food consumption (1–2 $mg \cdot g^{-1} \cdot day^{-1}$) of Lake of the Woods walleye during June, when trout-perch densities exceeded 400 $mg \cdot m^{-3}$, and by Shagawa Lake walleye when age 0 yellow perch concentrated near aquatic macrophytes shows that walleye required prey in open water to maintain daily food consumption between 3–4% of body weight.

In contrast to walleye, sauger relied primarily on trout-perch as an energy source, indicating a closer association with the bottom. Relative low food consumption rates, limited variation in feeding activity during the 24-h day and predation on trout-perch, a species associated with the cover provided by the lake bottom, suggests that rate of prey capture required to maintain food search behavior is lower for sauger than for walleye. Evidence that food search behavior is dependant on capture success has been provided by Ware (1972) who found rainbow trout (*Salmo gairdneri*) feeding success was limited by cover conditions and food searching waned if rate of prey capture declined below a critical level. Ali and Anctil (1968) found differences in the structure of the retina provide sauger with improved vision under reduced light conditions. This physiological difference would increase the probability for selection of feeding behavior in sauger effective in capturing demersal prey. Differences in feeding behavior identified by this study would appear to be important to the coexistence of walleye and sauger in freshwater communities.

Available information suggests walleye are adapted to maintain daily food consumption between 3–4% of body weight and this level of feeding results in increased food availability, annual consumption, survival, and food conversion efficiency. Crepuscular and night active feeding resulted in daily food consumption between 3–4% of body weight during July and August when prey density and temperature were not limiting and day-active feeding would have resulted in higher feeding rates. However, increased predation during July or early August would reduce age 0 yellow perch population densities. In Shagawa Lake (Table 3), Lake of the Woods (Swenson and Smith 1976), and Oneida Lake (Forney 1974) predation by walleye or sauger was the principal factor limiting prey survival and the greatest effects occurred during early summer when they fed on small size prey. Cannibalism occurred in Shagawa Lake and Oneida Lake

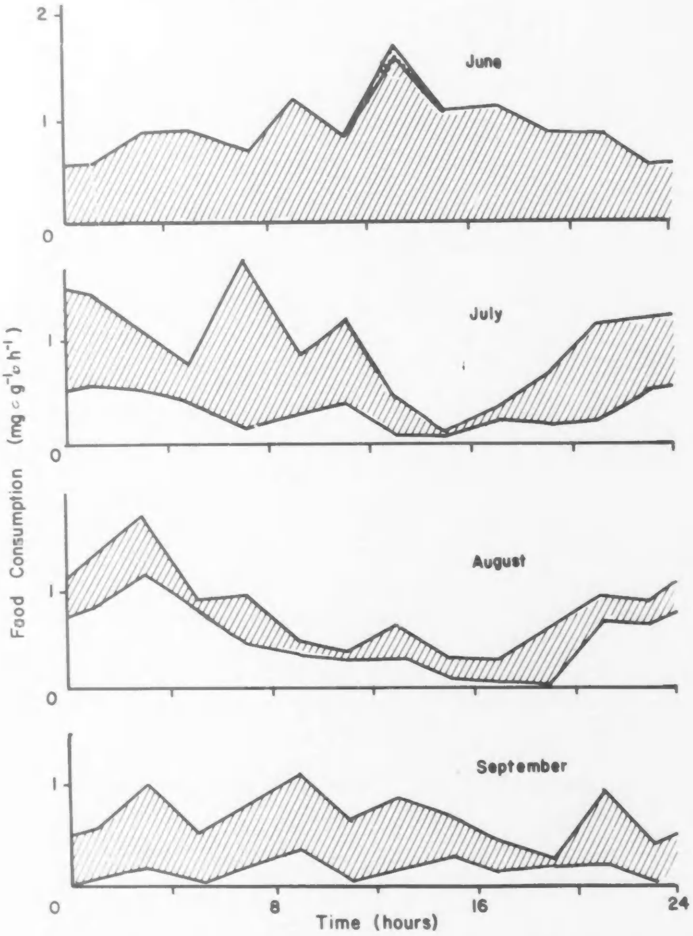

FIG. 5. Hourly food consumption ($mg \cdot g^{-1} \cdot h^{-1}$) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Lake of the Woods sauger.

(Forney 1976) during late summer if prey density was low. If prey densities were high, cannibalism was limited (Forney 1976) and food consumption was maintained between 3–4% of body weight even at lower late September temperatures. During late September feeding throughout the day resulted in higher stomach volumes, high digestion efficiency, and maintenance of food consumption between 3–4% of body weight. Kelso (1972) found food consumption by walleye in the laboratory was reduced to maintenance levels at 12°C, the temperature at which food consumption must be temperature limited. Gross food-conversion efficiency of Lake of the Woods walleye was 22% with rations approximating 3% of body weight and 17% at lower June rations of 1% of body weight (Swenson and Smith 1973). Thompson (1941) showed consumption rates between 3–4% of body weight resulted in maximum conversion efficiency in largemouth bass (*Micropterus salmoides*).

Aquatic vegetation appeared to reduce availability of prey in Shagawa Lake. Lower daily food consumption occurred during September when age 0 yellow perch were abundant but associated with aquatic macrophytes. Age 0 walleye moved into deep water with older age groups in both Lake of the Woods and Shagawa Lake at

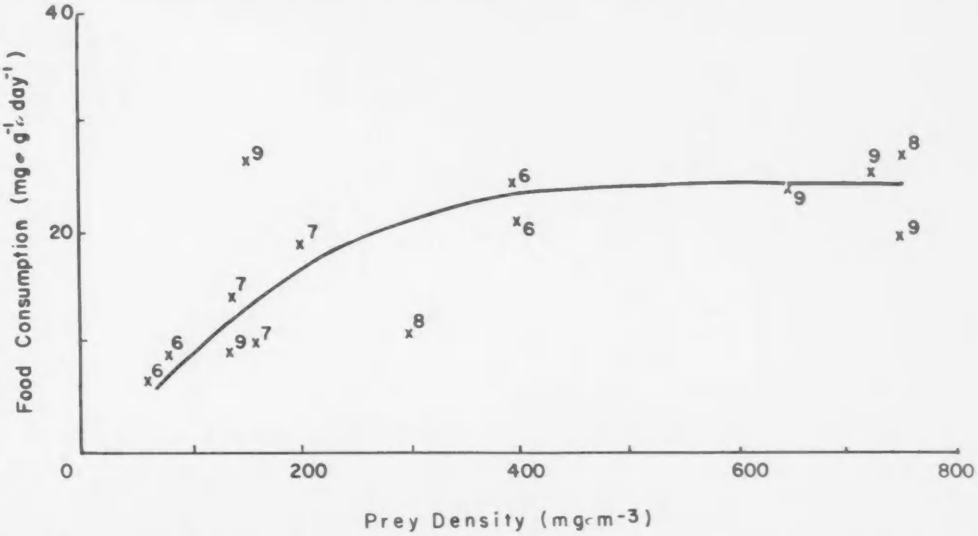

FIG. 6. Relations between daily food consumption rate of Lake of the Woods sauger and prey density during periods of moderate wave action. Numerals indicate calendar months.

this time. Cannibalism by walleye occurred only in open water areas of Shagawa Lake where density of yellow perch was lower. Observations from Shagawa Lake suggest aquatic macrophytes may also be a major factor limiting predation by walleye on Centrarchidae.

Midday feeding activity was reduced by high light intensity. In lakes where prey densities would not result in daily food consumption between 3–4% of body weight through crepuscular and night feeding activity, light limited feeding could restrict growth. The increased water clarity of Shagawa Lake associated with tertiary treatment of sewage since 1973 appears to limit midday feeding as a result of increased light penetration and to reduce food availability as a result of expanded macrophyte distribution. However, daily food consumption was maintained at high levels due to high prey density during most of the growing season. If prey fish populations decline, major changes in daily food consumption, growth, and survival would occur. Walleye abundance was low in the clear water of Lake Superior but increased with red-clay turbidity. High light intensity related to clear water conditions restricted the distribution of Lake Superior walleye and their use of a major food resource.

Figure 3 appears to represent a general relationship between walleye daily food consumption and prey density for a variety of lake systems and could be used to estimate food consumption of walleye in other lakes. Information provided herein on the factors influencing prey availability could be applied in measuring density of available prey from trawl catches for other waters. Food consumption rates could then be estimated from the prey density measurements and the relationship between daily food consumption and prey density developed for the three study waters (Fig. 3). Although estimates of food consumption derived in this manner may lack precision, they could be obtained with limited effort and should be valuable to lake management. Lakes with prey densities high enough to support daily food consumption rates between 3–4% of body weight throughout most of the growing season could be managed to their high production potential. Management of lakes with low food availability should be directed at increasing food availability rather than walleye population numbers because this study and others (Forney 1976; Swenson and Smith 1976) have shown that cannibalism or predation will limit walleye populations in lakes with limited food resources. Lakes characterized by low prey density may be best managed for another species.

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Unexploited Percid Populations of West Blue Lake, Manitoba, and their Interactions[1]

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West Blue Lake, Manitoba, essentially unaffected by man, sustains populations of yellow perch, *Perca flavescens*, and walleye, *Stizostedion vitreum vitreum*, which interact in two fundamental ways: perch are a major source of energy for walleye and the two species share common food organisms.

Perch adults, juveniles and fry generally contributed 80–90% of the energy required for the annual walleye production (340 kg) and, on the basis of conversion experiments, provided for at least 1.7 $kg \cdot ha^{-1}$ of the observed production of 2.1 $kg \cdot ha^{-1}$. The brief summer growth period, combined with moderate mortality, caused biomass to reach a maximum in early fall at which time production ceased.

Although walleye utilized yellow perch as its basic energy supply, behavioral differences tended to offer protection to juvenile and adult perch. Walleye were active at night, whereas older perch were inactive. Age 0 perch, during their epilimnetic phase, on the other hand, were active at night and vulnerable to walleye predation providing at least 18% of the observed walleye production.

Walleye and yellow perch shared the same food resources although at different times and to different degrees. This competition was most intense between walleye (>25 cm) and adult perch (>12 cm). A main food item shared was amphipods. Most other food items (sticklebacks, mayflies, crayfish) were also shared but none in equal proportions by the two percids.

Neither of the percid species showed a preponderance of older individuals and both showed evidence of strong and weak year-classes — walleye to a greater degree. Also, for walleye at least, production was only 2.1 $kg \cdot ha^{-1}$, and biomass appeared to be stable, approximately 900 kg. Growth for both species was less than most other percid communities and was restricted to a brief, ≈80 day, period.

Key words: unexploited, yellow perch, walleye, feeding, behavior, production, population structure

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Le lac West Blue, Manitoba, essentiellement inaffecté par l'homme, supporte des populations de perchaudes, *Perca flavescens*, et de dorés jaunes, *Stizostedion vitreum vitreum*, qui agissent les unes sur les autres de deux manières fondamentales: la perchaude est une source majeure d'énergie pour le doré jaune, et les deux espèces se nourrissent des mêmes organismes.

Les adultes, les jeunes et les alevins de perchaude fournissent généralement 80–90% de l'énergie requise pour la production annuelle de dorés jaunes (340 kg) et, sur la base d'expériences de conversion, sont responsables d'au moins 1.7 $kg \cdot ha^{-1}$ de la production observée de 2.1 $kg \cdot ha^{-1}$. La brève période estivale de croissance, couplée à une mortalité modérée, fait que la biomasse atteint un maximum au début de l'automne, alors que la production cesse.

Bien que le doré jaune utilise la perchaude comme source première d'énergie, des différences dans le comportement donnent aux jeunes perchaudes et aux adultes une certaine protection. Le

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doré jaune est actif pendant la nuit, alors que les perchaudes plus âgés sont inactives. D'autre part, les perchaudes d'âge 0, durant leur phase épilimnétique, sont actives durant la nuit et vulnérables à la prédation par le doré jaune, contribuant au moins 18% de la production observée de dorés jaunes.

Le doré jaune et la perchaude se partagent les mêmes ressources alimentaires, bien qu'à des époques et à des degrés différents. Cette compétition est plus intense entre les dorés jaunes (>25 cm) et les perchaudes adultes (>12 cm). Un des principaux item ainsi partagés sont des amphipodes. Les deux espèces se partagent également la plupart des autres item alimentaires (épinoches, phryganes, écrevisses), mais aucun en proportions égales.

Il n'existe chez ni l'une ni l'autre de ces percidés une prépondérance de vieux individus, et les deux espèces comprennent de fortes et de faibles classes d'âge — à un plus grand degré chez le doré jaune. De plus, du moins pour le doré jaune, la production n'est que de 2.1 kg·ha^{-1}, et la biomasse semble stable, environ 900 kg. La croissance des deux espèces est moindre que celle de la plupart des autres communautés de percidés et est limitée à une brève période, ≈80 jours.

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WEST Blue Lake, Duck Mountain Provincial Park, Manitoba, favors identification of "natural" population characteristics and interactions among species. The lake was essentially unfished before the initiation of research in 1966 and, except for one year in 1971–72, the Provincial Government has prohibited all fishing other than experimental netting. Consequently, seasonal variations in biomass and productivity (Kelso and Ward 1972) were identified in the absence of the complicating effects of a fishery. The lake lacks an outlet and permanent inlet streams (Ward and Robinson 1974), thus eliminating problems associated with immigration and emigration.

This paper describes the unperturbed yellow perch and walleye populations and their competitive and predator–prey interactions. Results derive from three sources: previously unpublished data, accepted student theses and previously published papers. We have attempted to reassess the published material relating it to recent information and the objectives of this paper.

Description of the lake — The lake, located (see Ward and Robinson 1974) at an altitude of 670 m, is long, narrow, steep-sided and has no outlet. The maximum depth is just over 30 m and the mean depth is 11.3 m. The area is 160 ha. The littoral zone is limited primarily to the sills separating the basins of the lake.

During a 10-yr period the lake level has risen by about 1 m but annual fluctuations are minimal (15–20 cm).

Ice usually forms in mid-November and leaves the lake in mid-May. A maximum ice thickness of about 1 m occurs in March.

Thermal stratification begins usually in late May and by summer the metalimnion extends from approximately 6 to 10 m (Ward and Robinson 1974). At this time, the mean epilimnion temperature reaches 20°C.

The lake is at least partially meromictic. By late summer little or no oxygen remains below 25 m although oxygen is generally not depleted in the top 10 m.

Alkalinity, measured as $CaCO_3$, averaged 136 mg·ℓ^{-1} during 1974. pH values for the epilimnion and upper hypolimnion in summer ranged from 8.0 to 8.6 and from 7.0 to 8.0, respectively (Ward and Robinson 1974).

The most abundant submerged macrophytes are *Potamogeton richardsonii, Potamogeton pectinatus, Myriophyllum alterniflorum, Magalodonta beckii,* and *Chara vulgaris.* The mean daily macrophyte productivity for mid-May to late August, essentially representing annual production, is 72 mg C·m^{-2}·day^{-1} (Love 1974).

Five phytoplankton species predominated throughout the year: *Cyclotella bodanica, Asterionella formosa, Dinobryon sertularia, Anabaena spiroides,* and *Aphanizomenon flos-aquae.* Highest primary productivity generally occurred in early spring soon after the ice had left the lake (Ward and Robinson 1974). Largest values, over 800 mg C·m^{-2}·day^{-1}, occurred about May 15 in both 1971 and 1972.

Zooplankton form a simple community composed of three predominant species *Daphnia pulicaria, Cyclops bicuspidatus,* and *Diaptomus siciloides.* Less common zooplankters are *Epischura lacustris, Mesocyclops edax, Bosmina* sp., and *Chydorus* sp. *Daphnia pulicaria* is the predominant zooplankter in spring, summer, and fall.

Major components of the benthos are amphipods, *Gammarus lacustris* and *Hyalella azteca*

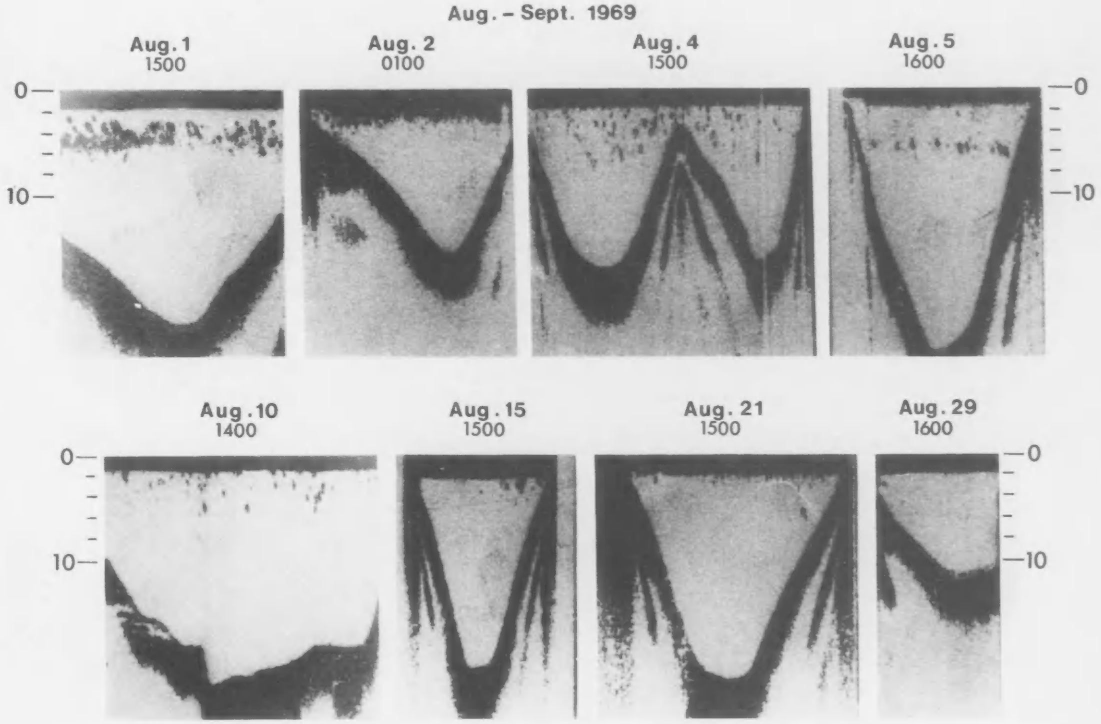

FIG. 1. Changes in pelagic distribution of yellow perch fry as shown by echograms, August 1969.

(Biette 1969), and crayfish *Orconectes virilis*. The chironomid *Tanytarsus* sp. and the ghost midge *Chaoborus flavicans* are also seasonally present.

In addition to perch and walleye, the northern pike, *Esox lucius*, and the brook stickleback, *Culaea inconstans*, are present but not abundant. A few lake trout, *Salvelinus namaycush*, still survive from introductions made before 1967.

West Blue Lake seems to lie near the boundary between oligotrophy and mesotrophy in terms of its phytoplankton productivity and biomass. In comparison with extremely oligotrophic Char Lake and polluted Meretta Lake in the Canadian Arctic (Kalff and Welch 1974) the lake is highly productive. On the other hand, the relation between annual primary productivity and annual average chlorophyll *a* (46 g $C \cdot m^{-2}$ and 3.8 mg chlorophyll $a \cdot m^{-2}$) places it near the boundary between oligotrophy and mesotrophy according to Vollenweider et al. (1974).

The morphoedaphic index (Ryder et al. 1974), 16.4, lies well below the optimum of 40 but places West Blue Lake in the upper range for north temperate lakes. It predicts a fish yield of 3.9 $kg \cdot ha^{-1} \cdot yr^{-1}$. Kelso and Ward (1972) estimated annual walleye production in 1969–70 to be 2.1 $kg \cdot ha^{-1}$. Since perch would add significantly to the calculated walleye production, the index provides a close approximation of potential production.

Yellow Perch Fry

Seasonal distribution — Throughout the summer, young perch were abundant in surface waters. Fry were first captured in the epilimnion in early June when they averaged 5.9 mm in length in 1975 and 5.6 mm in 1974. In early August, 1969, at about 30 mm in length when the typical "barred" color pattern of adults was developing, mid-lake catches declined while numbers increased in littoral areas (Wong 1972). The epilimnetic period, from mid-June to early August (Fig. 1), was followed by ingress to littoral areas as reported elsewhere (Echo 1954). In 1974 and 1975, onshore movement at about 30 mm occurred from mid-July to early August.

A scattering layer, shown by echograms (Fig. 1), associated with high tow net catches of fry between 2–6 m disappeared coincident with decreases in tow net catches. By late August, young-of-the-year were caught in gill nets along with juveniles and adult perch.

Diel movement — Perch fry were either more vulnerable to capture in the dark than in daylight or there was diel movement (Fig. 2). When surface tow net catches were low (Fig. 2), a scattering layer (Fig. 3) was distinct and occurred well below the surface; conversely, when surface catches were high, the scattering layer was diffuse and partially merged with the transmission line. Tow net catches supported the presumed diel migration between 0 and 5 m as daylight catches at the surface were low (5.5–36.2% of the total catches) and catches made after sunset constituted the major fraction of total catches. Although zooplankton (Boden 1962) and *Chaoborus* sp. (Teraguchi and Northcote 1966) produce sonic back-scattering, zooplankton sampling and net tows at known depths led to the conclusion (Wong 1972) that perch fry were the primary cause of the scattering layer.

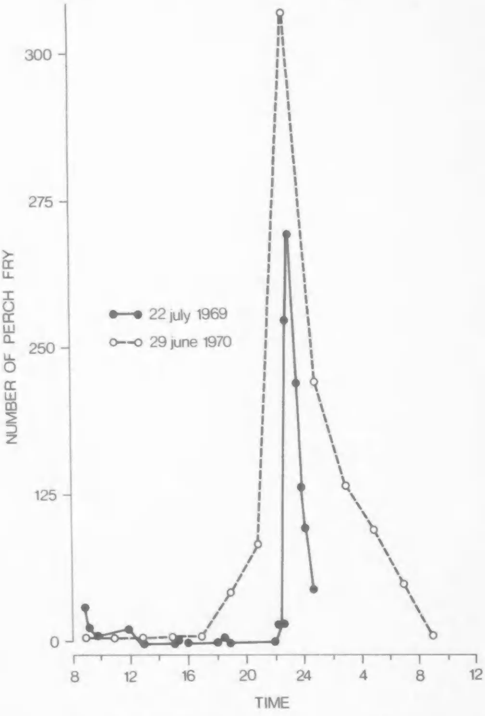

FIG. 2. Diel surface tow net (0.5 m diameter) catches of yellow perch fry July 1969 and June 1970.

Growth — From data collected in 1969 and 1974, fry were found to triple in length and increase in weight by a factor of 9 from July 1 to August 31. Average increases in length and weight were 38 mm and 1.8 g. Comparison of the two seasonal growth curves $L = 14.1e^{0.022t}$ (1969) and $L = 20.9e^{0.021t}$ (1974) indicated no significant difference ("t" = 0.74 ns, df = 43). The intercept from the regression was similar to the size first observed in the lake, 5.6 mm.

Weekly specific growth rates (Fig. 4) increased when perch fry were epilimnetic and then declined when perch fry became littoral. Data from 1974 and 1969 showed that the rise and fall in specific growth rates was a common occurrence. The epilimnion, then, appeared to favor yellow perch fry morphologically (in early stages coloration is favorable to survival in epilimnion) and metabolically (high growth rate).

Food and feeding — Fry utilized a narrow range of food items and relied largely upon zooplankton (Table 1). *Daphnia pulicaria* occurred in all but a few of the stomachs examined. Copepods, *Cyclops bicuspidatus* and *Diaptomus siciloides*, occurred less frequently (Table 1). During the early postlarval phase, dipteran pupae were infrequently found.

Amphipods, *Gammarus lacustris* and *Hyalella azteca*, occurred in stomachs only in August after fry had moved to littoral areas and after weekly specific growth rates (Fig. 4) had decreased. Fry examined in 1974 supported Wong's (1972) conclusion that, during most of the epilimnetic period, *Daphnia* sp. were predominant in stomachs. *Daphnia pulicaria* contributed 77–96% of the total caloric content in each stomach (Table 1) and copepods, although prominent, contributed less energy (1–19%).

Although stomach contents were high in advance of high weekly specific growth rates (Fig. 4), the patterns were similar. When specific growth rates tended to slow as perch fry began utilizing littoral habitats, energy content in stomachs (still largely *D. pulicaria*) decreased relative to total body caloric value. Also, perch fry appeared to feed continuously at least during early summer as stomach contents remained above 1% of the body caloric value.

Before mid-July, perch fry selected *D. pulicaria* which were smaller than those in plankton collections (Wong and Ward 1972). Subsequently, mean sizes in stomachs and in plankton catches were similar. Apparently *D. pulicaria*

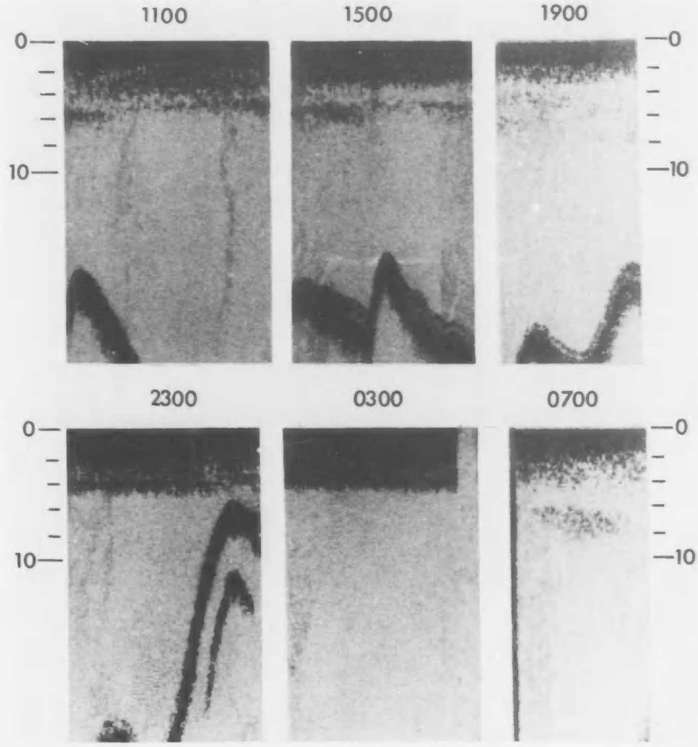

FIG. 3. Echograms obtained coincident with surface net tows, June 1970, showing diel changes in the scattering layer (perch fry).

longer than 1.3 mm could not be readily ingested until mid-July when perch fry were approximately 18 mm long. The heterogonic relation between growth in mouth and body size enabled perch fry to quickly utilize, as a major energy source, the predominant zooplankter (Wong and Ward 1972).

Yellow Perch Juveniles and Adults

Marked yellow perch did not randomly mix with the unmarked population. Releases and subsequent recaptures indicated the occurrence of at least temporary subpopulations thus precluding abundance estimates.

Juvenile (<120 mm) and adult (>120 mm in fork length) yellow perch were found to be active only during the day (Fig. 5). Although catch rates varied seasonally (Fig. 5), they tended to be diurnally bimodal with largest catches in the evening. No juveniles or adults were caught after nightfall although considerable effort was expended. At night, perch were observed (Falk 1971) to remain motionless either on the bottom or among submerged vegetation.

Age and growth — Age-class structure of the perch population was derived from gillnet catches made after annulus formation in 1969 and 1970. Yellow perch appeared to survive for 10 yr with most, 96%, being less than age 7 (Fig. 6). Few age 5 individuals were found, suggesting the occurrence of weak year-classes.

Perch size (Fig. 6) in part reflected age-class structure as abundant age 1 fish formed a large cohort between 50–90 mm whereas few large, 200 mm, and older, fish existed in the population. Recruitment (Fig. 6) appeared to be irregular.

Greatest annual increases in length occurred in the first several years of life. Older fish increased in length at a lesser rate than young ones but because of the relationship between length and weight ($\log_{10}{}^{W} = -5.509 + 3.052 \log_{10}{}^{L}$) increases in weight were correspondingly greater.

Food and feeding — Amphipods dominated juvenile perch stomach contents during July

TABLE 1. Frequencies of occurrence (%) of items in perch fry stomachs (column 1) and their percentage contributions of mean total caloric content to each stomach (column 2) from July 1969 to June 1970.

	Daphnia		Copepods		Nauplii		Amphipods	
Date	1	2	1	2	1	2	1	2
				1969				
July 1–5	99.9	86.9	58.6	13.2	—	—	—	—
July 6–12	100.0	87.5	26.8	12.5	—	—	—	—
July 13–19	100.0	91.3	13.6	8.7	—	—	—	—
July 20–26	100.0	94.5	23.3	5.5	—	—	—	—
July 27–Aug. 2	100.0	93.9	25.5	6.1	—	—	—	—
Aug. 3–9	100.0	94.0	38.7	6.0	—	—	—	—
Aug. 9–16	100.0	96.1	42.1	3.9	—	—	—	—
Aug. 17–23	100.0	92.3	25.0	2.6	—	—	65.6	4.5
Aug. 24–30	100.0	94.3	21.2	0.6	—	—	40.4	5.1
				1970				
June 15–29	100.0	77.1	100.0	19.2	100.0	3.7	—	—

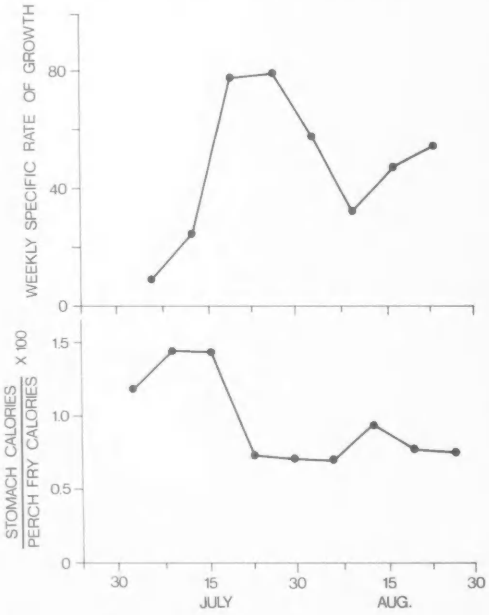

FIG. 4. Weekly specific growth rates (*upper*) and caloric relation between stomach contents and perch fry (*lower*) during July and August, 1969.

(Table 2) and were common in stomachs examined at other times. Cladocerans were the major contributor, 69% by weight, to the juvenile perch diet in September but were also common during June. Fish, including yellow perch, were common in stomachs and at times made up 30% of total stomach weight. *Orconectes* sp., dipterans, and other insects occurred infrequently.

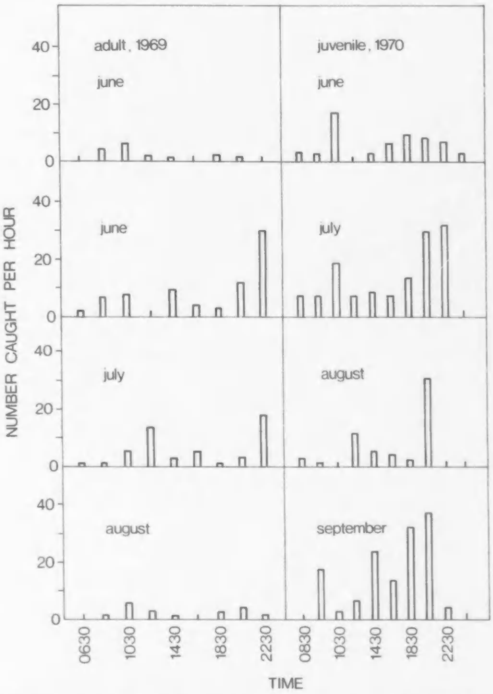

FIG. 5. Diel capture rates in gill nets of juvenile and adult yellow perch, 1969 and 1970.

Adult perch fed mainly upon amphipods and dipterans during June, sticklebacks during July and *Orconectes* sp. during August (Table 2). *Daphnia pulicaria* was not common in the diet of adult yellow perch. Adults tended to utilize a broader spectrum of food items (Table 2) al-

TABLE 2. Percent of total stomach content weights provided by items occurring in yellow perch stomachs during various periods, 1969 and 1970. Stomachs reported for 1969 are adults and those reported for 1970 are juveniles.

Item	Early June	Late June		Late July		Late August		Mid-September
	1969	1969	1970	1969	1970	1969	1970	1970
Hyalella	60	1	11	1	46	1	21	4
Gammarus	11	5	23	11	23	8	9	8
Daphnia	0	5	32	0	0	2	0	69
Diptera	25	52	11	1	1	0	1	1
Hemiptera	0	1	0	1	0	0	0	0
Odonata	0	18	0	5	0	0	0	0
Perca	0	0	3	8	29	14	30	0
Orconectes	2	0	0	5	1	54	7	10
Culaea	0	20	10	41	0	19	30	1
Other insects	3	0	1	0	1	3	3	0
Misc.	1	0	0	30	0	0	0	8
Total stomach content weight (g)	8.24	30.38	2.74	20.44	7.83	11.40	3.98	5.37
No. stomachs with food	31	87	72	71	124	51	49	86

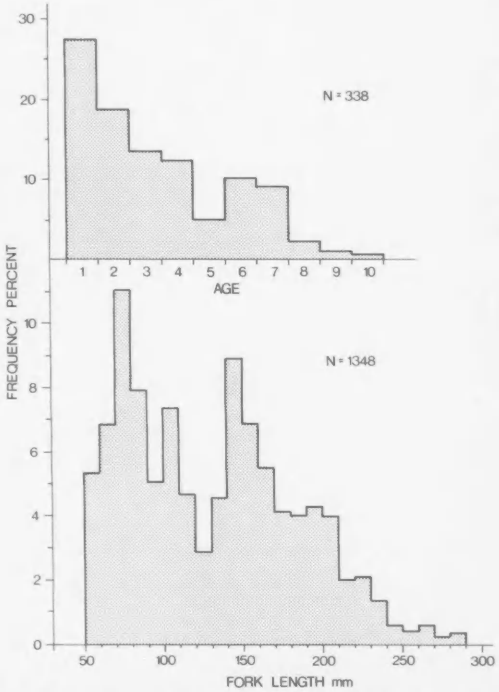

FIG. 6. Age and length frequency distributions for yellow perch, catches were made only in July, 1969 and 1970.

though one item usually predominated in stomachs.

Contributions, by weight, of the primary food taxa varied by a factor of up to 2 between 1969 and 1970 (Table 2). Differences in feeding were also apparent between juveniles and adults and real differences appeared to exist from year to year and between juveniles and adults.

Because migration and movement patterns of yellow perch are variable and complicated (Scott 1955) and probably affect feeding behavior, stomach contents of juveniles captured in different basins and at different depths were compared. Comparisons between locations indicated that, in general, no significant difference (χ^2 tests between locations, $P > 0.05$) in feeding existed between basins.

Utilization of both limnetic and littoral food sources is known to occur, but in this study amphipods predominated in juvenile perch stomachs, those from deeper water containing largely *Gammarus* sp. and those caught inshore containing largely *Hyalella* sp. Since Biette (1969) found *Gammarus* sp. associated with *Chara* sp. and deeper water and *Hyalella* sp. associated with *Potamogeton* sp. and shallow water, the observed differences in stomach contents were expected.

Stomach fullness and stomach content per unit of body weight changed in both juveniles and adults on a diel basis (Fig. 7), as observed also by Hasler and Bardach (1949) and Keast and Welch (1968). Yellow perch with empty stomachs predominated in early morning catches (Falk 1971). During June, stomach contents quickly increased from 0630 to 1030 h, and gradually decreased throughout the day. This diel pattern of stomach fullness was apparently bimodal for juveniles in July and September and for adults in July and August. The change (Fig. 7) in predominance of frequently ingested food

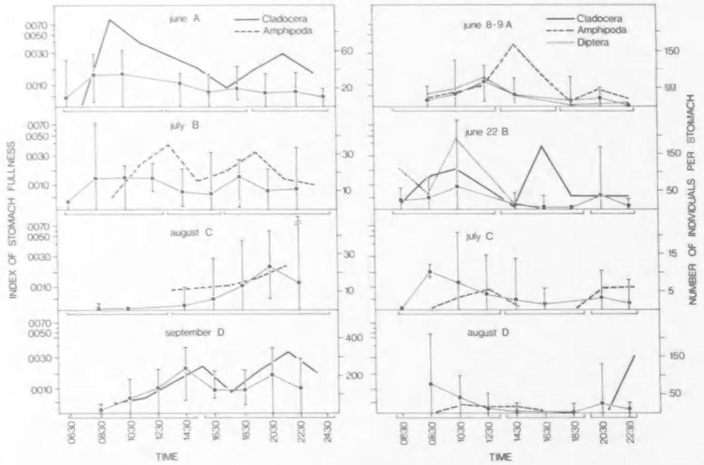

FIG. 7. Diurnal indexes of stomach fullness and number of selected prey species for June to September of juvenile (*left*), 1970, and adult yellow perch, 1969.

items (Falk 1971) supported bimodality of feeding.

Weight of stomach contents increased with increasing length of yellow perch as follows: $W_s = 0.043\ L^{2.366}$ where W_s is stomach content weight and L is fork length. A t-test between the observed exponent, 2.366, and that from the length–weight relationship, 3.05, indicated a significant difference ($t = 2.418^{**}$ df $= 13$). Consequently, weight of stomach contents increased with length and hence weight but not in direct proportion to the latter.

Falk (1971) also found that prey consumed tended to vary with predator size. Although the range in perch size was limited, only 60–119 mm, cladocerans were apparently consumed more by smaller fish (60–99 mm). Conversely, amphipods were consumed equally by all sizes even though *Hyalella* sp. was eaten by smaller perch and *Gammarus* sp. by larger perch. Larger yellow perch tended to be piscivorous because perch and brook stickleback constituted the bulk of the diet of perch 120 mm in length.

Walleye

Age-class structure — Strong year-classes were apparent (Fig. 8) in the population but factors contributing to year-class strength are largely unknown. Abundant year-classes carried through to later years (Fig. 8). The age distribution was not stable and probably reflected spawning success (Ward and Clayton 1975). Lack of older fish before 1974 was unlike other undisturbed populations (Carlander 1945; Kennedy 1954; Forney 1961; Johnson 1972) which tended to be stable and long-lived.

Mortality — Instantaneous daily mortality (Table 3) was greatest between September and October and lowest between May and June. Survival — consequently mortality — applied to the whole recruited (>25 cm) population (Kelso and Ward 1972). Annual mortality estimates, then, indicate that only 20% of the initial population would survive. Natural walleye mortality found in West Blue Lake far exceeded that reported for Oneida Lake and Lake Erie (Forney 1967; Regier et al. 1969). Observed walleye mortality agrees approximately with data reported by Kennedy (1954) for an unexploited lake trout population, 35–65%, and by Ricker (1947) for a variety of species, 19–80%.

Population characteristics and production — Annual production of walleye flesh, 340 kg, occurred almost totally between June and October and followed a pattern related to seasonal growth (Kelso and Ward 1972). Total annual production resulted largely from the 1967 (180.41 kg) and 1964 (61.21 kg) brood years. The 1967 stock, however, contributed 40% less to population biomass than did the 1964 stock. Although abundance increased between May 1969 and May 1970 (Table 4) biomass was approximately similar. Production during fall and winter

TABLE 3. Survival and daily instantaneous mortality rates of walleye for various periods, 1969 and 1970.

Period	Survival rate (s)	Instantaneous mortality per day (i)
May 14–20, 1969		
	$s_{12} = 0.999\ (\pm\ 0.465)^a$	$i_{12} = 0.00003$
June 16–22		
	$s_{23} = 0.835\ (\pm\ 0.546)$	$i_{23} = 0.0022$
Sept. 3–12		
	$s_{34} = 0.664\ (\pm\ 0.421)$	$i_{34} = 0.0136$
Oct. 5–12		
	$s_{45} = 0.525\ (\pm\ 0.407)$	$i_{45} = 0.0028$
May 18–22, 1970		
		mean $i = 0.0045$

[a] One standard deviation of mean.

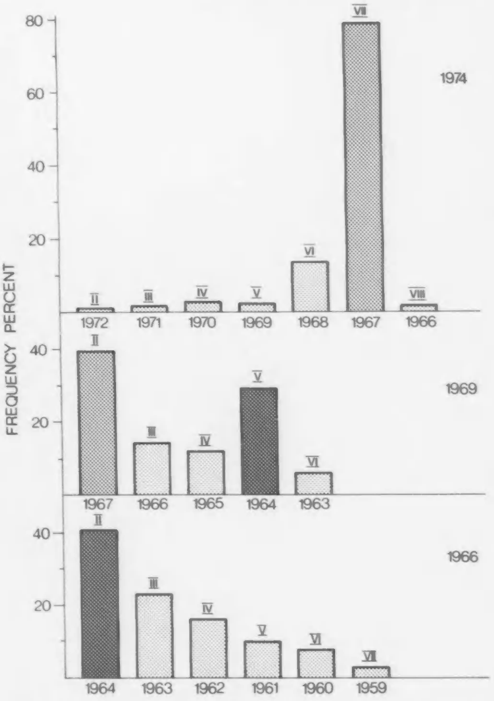

FIG. 8. Age-class structure of walleye for 3 yr between 1966 and present.

was either zero or negative. Others have found that most walleye production occurred in a limited period (Forney 1966) and that periodic losses in weight occurred over winter (Hile 1941).

The annual production for 1969–70 was 2.1 kg·ha^{-1}. Growth was similar from year to year (Glenn 1969; Kelso and Ward 1972 and recent data). However, as age-class structure is variable, it is unknown whether production both within and between years was similar to that described herein. However, since age-class structure of the population differed between 1969 and 1970 though biomass was similar, stability in at least standing crop appears to exist. A Minnesota walleye stock (Smith and Krafting 1954) during 1930–53 yielded mean catch of 2.8 kg·ha^{-1} and, assuming that catch approximated production, production in these two very different systems was similar.

Diel movement — During nocturnal netting experiments (Fig. 9), nearshore catches increased at dusk and decreased at dawn. Diel activity patterns can be interpreted from gillnet catches (Carlander and Cleary 1949) and when compared with concurrent echograms (Fig. 10), diel habits of walleye became clearer. Echograms obtained in early evening, August 23–24 indicated large targets near bottom and in midwater. As light intensity decreased, targets moved inshore and upwards in the water column and coincided with increases in gillnet catches (Fig. 9). Targets soon entered the near-field acoustics region and melded with the transmission line when gillnet catches were highest. As daylight increased, the reverse occurred until walleye were again offshore in midwater or on the bottom. Yellow perch were never caught after sunset in West Blue Lake (Falk 1971) and it seems unlikely then that the targets were perch. Recent telemetry studies (Kelso 1976) supported these observations and indicated that movement was limited to the relatively homothermous epilimnion.

Growth — During 1966–67 and 1969–70 most growth had occurred by mid-September (Fig. 11). Data from the 2 years were similar in that fish had attained similar percentages of their total annual growth by mid-September:

TABLE 4. Abundance, biomass, and production of the unrecruited (subscript 1) and recruited (subscript 2) walleye populations, May 1969 to May 1970.

	Abundance		Biomass (kg)		Production (kg)	
Date	N_1	N_2	B_1	B_2	P_1	P_2
May 14–20, 1969	1090	3656	703.1	907.9		
					−3.6	−6.3
June 16–22	1330	3893	725.3	930.6		
					140.4	307.1
Sept. 3–12	1350	3451	979.2	1303.2		
					22.3	38.4
Oct. 5–12	931	2331	639.1	834.4		
					0.8	1.0
May 18–22, 1970						
Totals					159.9	340.3

	Percent of annual growth	
Age	1966	1969
II	82	91
III	79	97
IV	65	81
V	60	82
VI	44	—

Little growth (Fig. 11) occurred in winter months. Increase in weight was less regular than increase in length and the youngest fish did not show greatest increases in total weight. During both years, age III and IV increased in weight at similar rates and showed similar gains.

Coinciding with seasonal increases in length and weight was a seasonal change in total body calories (Kelso 1973). Total body energy excluding gonads, 4550 cal·g^{-1} in spring, increased approximately 12% coincident with rapid summer growth in length and weight. No significant differences were found among age-groups vulnerable to capture. The age-independent caloric accumulation, probably in the form of fat deposits, must result from the natural growth and metabolic processes between May and October.

Food and feeding — To generally assess contribution to walleye (>25 cm) nutrition, 2 years of data were compared (Table 5). Yellow perch and brook stickleback contributed between 78 (1966) and 72% (1969) to walleye stomach contents. The next major contribution was provided by either crayfish (1966) or amphipods (1969). Although age 0 yellow perch were abundant in stomachs during both years, their early contribution by weight was considerably less than that provided by older perch.

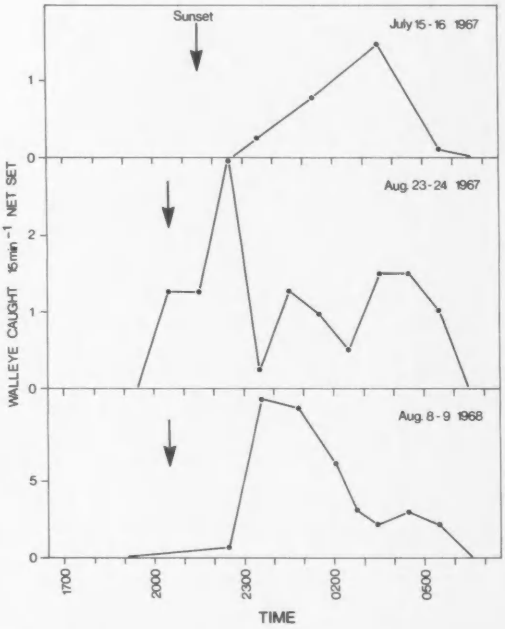

FIG. 9. Diel capture rates of walleye during three experiments, 1967 and 1968.

In diel samples, the number of fish with empty stomachs declined as night progressed (Fig. 12). During August, however, data suggested bimodality in feeding behavior. Although observed changes in distribution (Fig. 10) and catch rate (Fig. 9) may result from physiologic and behavioral response to light (Ali and Anctil 1968) the ingress into the littoral zone is opportunistically used for feeding.

Few species were utilized as food by walleye, yet seasonal differences occurred (Fig. 13 and Table 5). Amphipods were usually present in walleye stomachs but were most common in early spring and late fall when growth (Fig. 11) was slow. Walleye apparently capitalize upon the

TABLE 5. Contributions by number, weight, and percent of total weight of food items to walleye (>25 cm) stomach contents 1966 and 1969–70, all seasons of collection.

Organism	1969–70 Number	Weight (g)	%	1966 Number	Weight (g)	%
Amphipods	1205	35	12.8	383	19	3.3
Age 0 yellow perch	102	38	14.1	408	68	11.9
Older yellow perch	6	134	49.8	21	371	65.3
Orconectes	4	13	4.8	40	90	15.6
Leeches	5	14	5.0	7	3	0.6
Insects dragonfly nymphs mayfly larvae caddisfly pupae	626	11	4.1	56	5	0.9
Misc.		5	1.9		8	1.5
Brook stickleback (Unident. fish Glenn and Ward 1968)	27	21	7.6	7	5	0.8

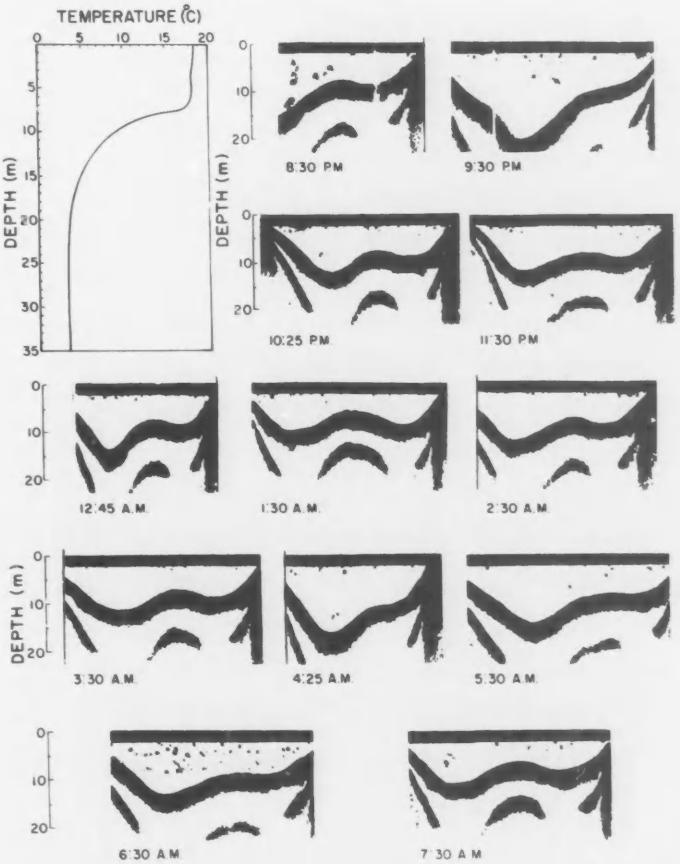

FIG. 10. Echograms obtained coincident with gillnet catches (Fig. 9) made to determine diel capture rates, 1967.

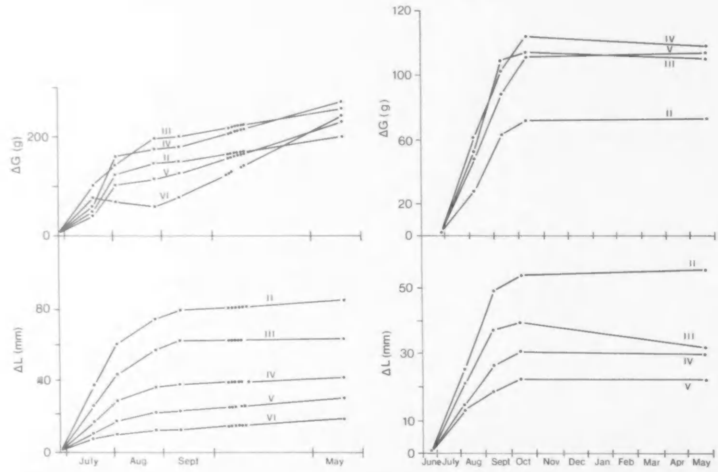

FIG. 11. Increases in length and weight of walleye of various ages during 1966–67 (*left-hand panel*) and 1969–70.

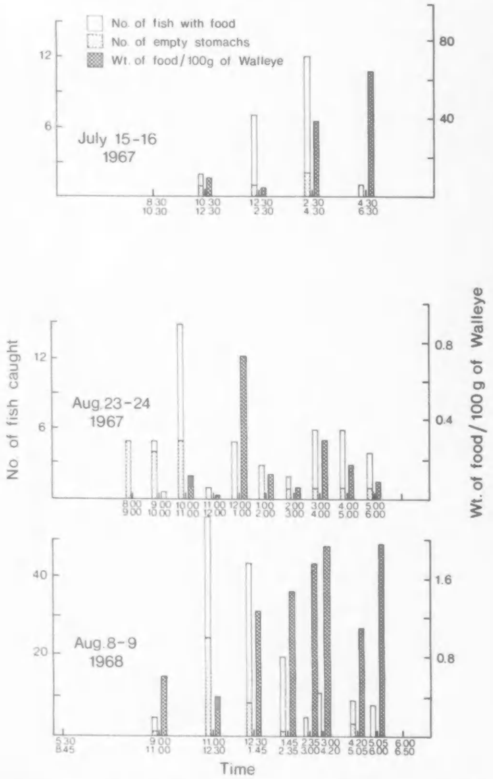

FIG. 12. Numbers of walleye with food taken at night, number with empty stomachs, and weights of food per 100 g of walleye on three occasions.

early period of amphipod abundance but in early summer they preyed more heavily upon age 0 yellow perch although amphipods were still abundant. The fact that walleye are opportunistic in their feeding is accentuated by the predominance of mayfly larvae (*Blasturus* sp.) in stomachs of walleye (Fig. 13) just before emergence of mayfly as adults. Walleye fed heavily upon age 0 perch at about the time fry developed vertical banding. Once perch fry reentered the littoral (Fig. 1), they became a major source of energy for walleye. "Older" perch, essentially littoral throughout the year (Falk 1971), are consistent contributors to walleye nutrition.

Knowledge of the disposition of ingested energy by walleye (Kelso 1972; Swenson and Smith 1973) is limited but generally supports observations on the West Blue Lake population. Assimilation efficiency decreased with increasing walleye size ($E = 96.85 - 0.0045\ W$, where E is assimilation efficiency and W is walleye weight) indicating that younger fish are most efficient. Furthermore, assimilation efficiency was higher, 15%, for fish than crustaceans (Kelso 1972) thus making the perch fry contribution more valuable to the critical summer growth period. In the laboratory, fish held at temperatures below 12°C fed only at maintenance levels, supporting the zero or negative production observed (Table 4) in the lake during late fall, winter, and spring.

General Discussion

Yellow perch fry in West Blue Lake inhabited a zone in which food was abundant and available

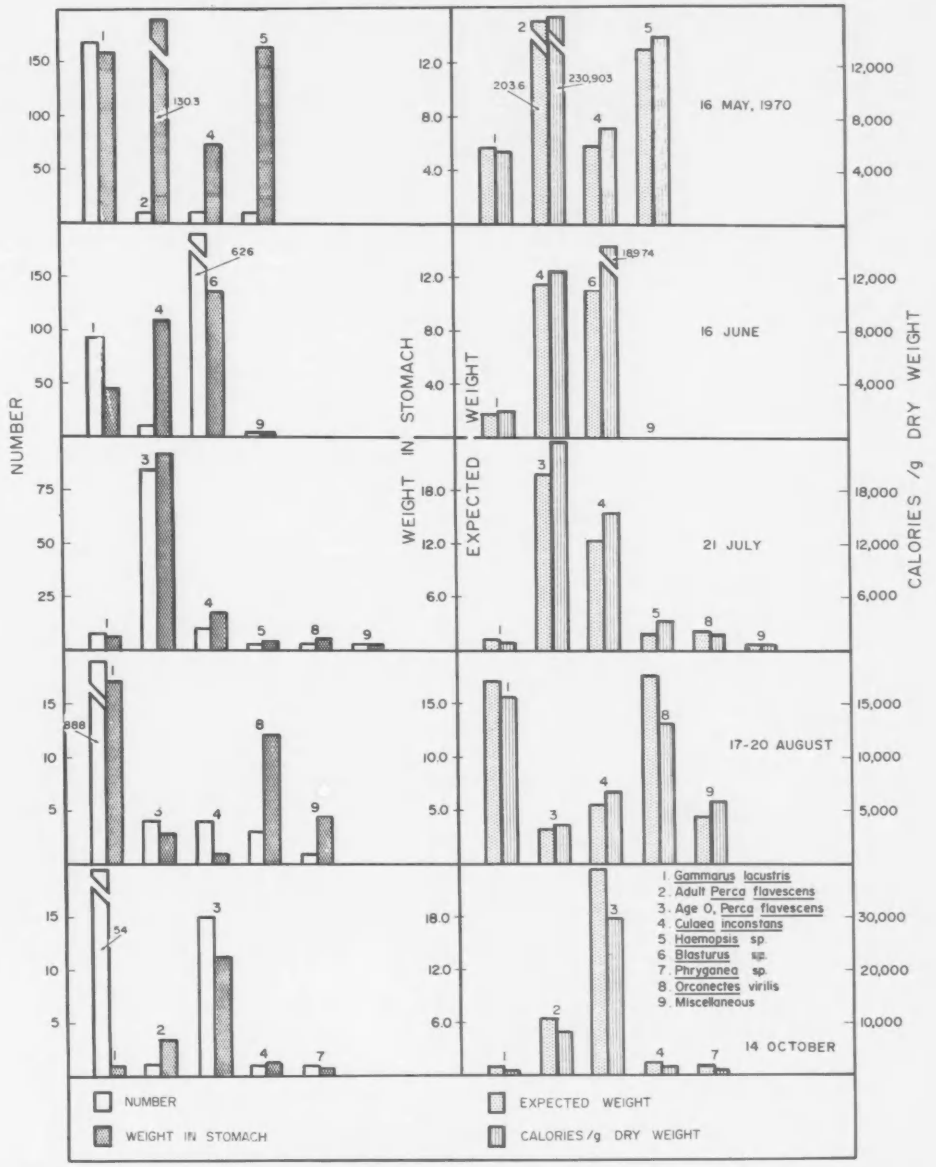

FIG. 13. Contributions of various organisms in number, weight, and caloric content to diet of walleye on five occasions, 1970.

at a critical time in their life. The offshore movement and the epilimnetic phase of life coincided with the maximum abundance of *Daphnia pulicaria.* This offshore dispersion seems to permit fry to take advantage of this food source and to minimize intraspecific competition for food which would have been more intense had the fry remained near spawning sites in the limited littoral area.

The decrease in growth rate (Fig. 4) accompanying the inshore movement seems a nonadaptive consequence. The only apparent adaptive advantage of the inshore movement is that the newly acquired barred color pattern is appropriate to survival in shallow water among aquatic plants and inappropriate to pelagic life (Wong 1972). Although the initial inshore movement seems inappropriate from a growth standpoint, in the long run the littoral zone offers the young perch two major advantages.

The occupation of the epilimnion by perch fry soon after hatching takes advantage of the high productivity and abundance of small rapidly reproducing food items. On returning to the littoral area, the now much less abundant age 0 perch fry have available a larger variety of larger organisms, occupying more than one trophic level, to utilize as food. Furthermore, the benthic community because it is more mature (Margalef 1963), is by definition, less unstable than the pelagic one and therefore less subject to extreme fluctuations in total abundance and biomass.

The transfer of larvae from a more mature system (the benthos) to a less mature one (the planktonic) and the return of the survivors to the mature system is a common occurrence, particularly in marine species and results in a net energy transfer from the less to the more mature system (Margalef 1963).

The majority of annual growth of walleye occurs in about 80 days ending by mid-September; during this period, yellow perch in West Blue Lake provide the major share of the energy required by walleye. Clearly then, yellow perch provide the largest portion of the energy required for walleye production, 80% or 1.7 of 2.1 $\mathrm{kg \cdot ha^{-1}}$. The estimated contribution of perch fry (18%) to the walleye diet is probably an underestimate as sampling was limited to only the period when fry were most abundant and as digestion time for fry was brief, probably resulting in higher predation rate.

Although walleye utilized yellow perch as their basic energy source, behavioral differences in the two percids tended to offer protection to juvenile and adult perch. As demonstrated, walleye were active at night and fed primarily after sunset (Fig. 9 and 10). Conversely, older perch were inactive at night and apparently rested on bottom until dawn. This inactivity may reduce the effectiveness of a nocturnal predator. Age 0 perch during the epilimnetic phase, on the other hand, were active at night near the surface and vulnerable to walleye predation. The degree to which walleye predation limits the abundance of either age 0 or older perch is unknown. Though older perch are also preyed upon by the small number of pike in the lake, walleye are the only predator taking significant numbers of age 0 perch.

In addition to the intense predator–prey relationship, yellow perch and walleye interact as competitors. This interaction is most intense between walleye >25 cm and adult perch. We have no information on the food of age 0 walleye. A main food item shared by the two percids is amphipods but walleye use them less than juvenile perch. Adult perch and walleye share the same foods but not in the same proportions. One obvious difference is that walleye feed primarily on yellow perch whereas yellow perch, though cannibalistic, utilize other foods to a greater extent.

Although the two percid species interact as stated there is no evidence that these interactions limit the abundance of either. Walleye year-class strengths varied greatly (Fig. 8), suggesting that walleye abundance in this culturally unaltered system depends primarily on spawning success. We are not aware of the factors affecting egg and fry survival but walleye fry introductions in 1971 and 1972 resulted in a 100% increase in the 1971 year-class and a very large 1972 year-class although the contribution made by native fish was insignificant (Ward and Clayton 1975). These results indicate that, in the long term, this unexploited walleye population is limited by low egg-to-fry survival. In the short term, in the absence of a fishery, the seasonal abundance is regulated by severe natural mortalities occurring in the fall (Kelso and Ward 1972).

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Percids of Lake Constance, a Lake Undergoing Eutrophication[1]

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HARTMANN, J., AND W. NÜMANN. 1977. Percids of Lake Constance, a lake undergoing eutrophication. J. Fish. Res. Board Can. 34: 1670–1677.

A review of literature suggested that yield of Eurasian perch, *Perca fluviatilis*, in Lake Constance was greatest with moderate eutrophication. During eutrophication (1950–76), changes also took place in food, growth, distribution, and diseases of perch. Differences in perch between Lake Constance and other German or Alpine lakes of various degrees of eutrophy were found with respect to growth, yield, the relation of growth to yield, food, and the relation of food to growth. Similarities were apparent for perch in these lakes in terms of their age composition, age at maturity, and mortality. Only limited data were available for pikeperch, *Stizostedion lucioperca*, mainly on stocking success, yield, and growth. The status of percids in Lake Constance indicates that eutrophication has led to conditions favoring percids.

Key words: Percidae, Lake Constance limnology, eutrophication, yield, *Perca fluviatilis*, food, growth, distribution, disease, *Stizostedion lucioperca*

HARTMANN, J., AND W. NÜMANN. 1977. Percids of Lake Constance, a lake undergoing eutrophication. J. Fish. Res. Board Can. 34: 1670–1677.

Une revue de la littérature suggère que le rendement en perches eurasiennes, *Perca fluviatilis*, dans le lac de Constance fut à son maximum alors que l'eutrophisation était modérée. Au cours de l'eutrophisation (1950 à 1976), il se produisit également des changements dans la nourriture, la croissance, la distribution et les maladies de la perche. Les perches du lac de Constance montrent des différences par rapport à celles d'autres lacs allemands ou alpins à divers stades d'eutrophie quant à la croissance, le rendement, la relation entre la croissance et le rendement, la nourriture et la relation entre la nourriture et la croissance. Il y a d'apparentes similitudes chez les perches provenant de ces lacs quant à la répartition des âges, l'âge de la maturité et la mortalité. Les données disponibles sur le doré, *Stizostedion lucioperca*, sont peu abondantes et se limitent en grande partie au succès des peuplements, rendement et croissance. La condition des percidés dans le lac de Constance indique que l'eutrophisation a créé des conditions favorables aux percidés.

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IN this paper, changes that took place with Eurasian perch (*Perca fluviatilis*) and other fish species in Lake Constance, while it was undergoing eutrophication, are reviewed. The changes concern food, growth, yield, distribution, spawning time, and diseases. Only limited data for pikeperch (*Stizostedion lucioperca*) are available. Also, data on percids of Lake Constance are compared mainly with those of other German or alpine lakes. Originally the main basin of Lake Constance was oligotrophic. But since about 1950 a progressive eutrophication has taken place and now the main basin is considered to be between meso- and eutrophic.

Description of Lake

Lake Constance, 395 m above sea level, is situated at the northern edge (47°N 09°E) of the Alps. The lake is shared by Austria, Germany, and Switzerland (Fig. 1).

The basins were formed by glacial erosion (Würm ice age, equivalent to Wisconsin in North America) rather than by structural deformation. Tertiary molasse (conglomerates, sandstone, marl) forms the basic lake framework with fill provided by Tillite material (Würm ice age) and well-bedded fine-grained lacustrine sediments (Holocene period) (Müller 1971).

Rivers entering the lake drain an area of 11,000 km^2 and provide 10^9 m^3 of water per annum to the lake. Two thirds of this is transported by the Rhine. Lesser rivers drain tertiary molasse and, to a lesser

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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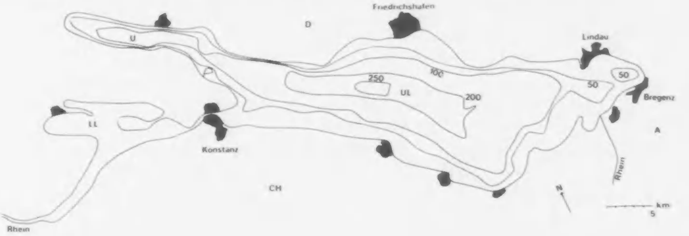

FIG. 1. Lake Constance bathymetry (m) showing: Konstanz (Constance); Rhein or Rhine (influx in the east); UL (Upper Lake); LL (Lower Lake); U — Lake of Uberlingen (part of the Upper Lake); broken lines are borders of Austria (A), Switzerland (CH), and Germany (D).

extent, tertiary volcanic areas (Müller 1971). One third (25% of this in the alpine region and 55% in the north) of the catchment area is used for agriculture and is artificially fertilized (Wagner personal communication).

The lake is comprised of two basins (Fig. 1), Upper Lake and Lower Lake, connected by the Rhine. The Upper Lake is the largest and deepest and has the longest flushing time (Table 1).

There are 1400 h of sunshine per year and the mean annual temperature is 8.6°C. Days having a mean air temperature exceeding 5.5°C total 229. Annual rainfall decreases from 1500 mm in the east to 800 mm in the west. Mean monthly water levels fluctuate up to 1.60 m with maxima in July and minima in December to February. For additional data see Nümann (1972).

Background limnology — The Upper Lake must be considered oligotrophic until about 1950, but since then cultural eutrophication (Table 2) has been apparent. Its state now is between meso- and eutrophic. The Lower Lake was mesotrophic until about 1950 but must now be considered eutrophic. Although its water comes from the Upper Lake, differences between them are significant.

Untreated municipal waste was the primary factor accelerating eutrophication. Not more than one third of the total added phosphorus was derived from agricultural practices. Most phosphorus was contributed by the 1.2 million people in the catchment area through sewage and detergents. These culturally induced nutrient changes were further complicated by engineering programs along the shoreline and regulation of river flow. Generally, nutrient addition was considered the major perturbing influence to Lake Constance (Int. Gewässerschutzkommn. 1975).

Assimilated carbon contents were similar, 0.6 to 1.1 $g \cdot m^{-2} \cdot day^{-1}$, in the Upper Lake and Lower Lake during September (Elster and Motsch 1966; Findenegg 1966). However, in June 1961–65, daily assimilated carbon in the Upper Lake (0.35 $g \cdot m^{-2} \cdot day^{-1}$) was half that of the Lower Lake. Production rates appear to have doubled from 1961 to 1965 (Findenegg 1966). Phytoplankton production per year recently amounted to 250,000 t in the Upper Lake and 35,000 t in the Lower Lake (Int. Gewässerschutzkommn. 1975).

TABLE 1. Morphometry of the basins of Lake Constance.

	Upper Lake	Lower Lake
Area, A		
Total (km^2)	476	63
0–10 m depth (%)	14	48
Depth (m)		
Maximum, Z_m	252	46
Mean, $\overline{Z}$	100	13
Volume (km^3), V	48	1
Shoreline length (km), S	171	90
Flushing rate (yr)	4.3	0.1
S/V	3.6	109
$\frac{S}{2\sqrt{A\pi}}$	2.2	3.2

Five decades ago, phytoplankton of the Upper Lake consisted almost exclusively of Diatomeae. Since then many diatom species have disappeared, e.g. *Cyclotella bodanica*, *C. socialis*, *C. comta*. Now, the algal community is frequently dominated by Pyrrophyceae, blue-green algae, and green algae. Concomitant with the species changes, standing crop increased approximately ninefold in the whole lake between 1935 and 1970 (Nümann 1972).

During eutrophication, the area inhabited by macrophytes increased in the Upper Lake and decreased in the Lower Lake (Int. Gewässerschutzkommn. 1975). Species changes also occurred as *Potamogeton perfoliatus* was replaced by *P. pectinatus* in the Upper Lake and both *Chara* sp. and *Elodea* sp. decreased in abundance in both parts of the lake.

In the Upper Lake, the species of planktonic crustaceans increased from 9 to 12 (Kiefer 1975). Furthermore, besides the introduction of new species, previously littoral zooplankters extended their habitats to limnetic regions. During the period of eutrophication, a copepod, important as a food item to whitefish and young perch, disappeared. Production also was greatly altered by eutrophication (Table 3).

Although a variety of benthic macroinvertebrates

TABLE 2. Selected physicochemical characteristics of Upper and Lower basins of Lake Constance before (1925–36) and after (1952–75) eutrophication. Averages are for one or more years.

	Upper		Lower	
Item	Before	After	Before	After
Color	bluish-green	olive-brown		
Transparency (m)	9.5	8.2	5.6	4.3
t_{max}/month surface	19.6		21.6	
t range bottom	4.0[a]		2.0–10.3	
Redox potential (mV)		570		
pH average	8.0	8.0	8.1	7.4[b]
maximum	8.4	8.7	8.6	8.8
Conductivity (mhos/cm)	262	263		279
Alkalinity (mg/ℓ $CaCO_3$)				
surface	95–125	95–129	100	100–125
bottom[c]	95–130	120–130	135	110–135
TDS/MEI (mg/ℓ)	190/1.9	190/1.9		190/15
Oxygen (%)				
maximum, surface	115	228	144	
minimum, bottom	82	29	5	0
Chloride (mg/ℓ)	0.4–1.6	4.0		
P_{tot} circulation period	10	88		540
P_{ortho} (mg/m^3)				
maximum, surface	1	70	10	86
maximum, bottom			170	248
N_{max} N as NO_3 (mg/m^3)	600	800	600	950
N_{max} NH_3 (mg/m^3)			500	1800

[a] Bottom temperature about 4°C throughout the year in the center of the upper lake.
[b] Minimum.
[c] In Upper Lake 200–250 m; in Lower Lake generally 20 m (deepest point of an arm).

are known in Lake Constance (Kiefer 1975), changes in Tubificidae were documented most thoroughly (Zahner 1964). In the Upper Lake, maxima of 3000 tubificids/m^2 were observed and later increased to 177,000/m^2. Among the benthic macroinvertebrates, an accidental introduction of a gastropod, *Dreissena polymorpha*, was detected about 1966 (Int. Gewässerschutzkommn. 1975) and has resulted in densities up to 10^4 individuals/m^2.

Coincident with changes occurring in general in other biota, fish catches have changed from coregonids to perch and cyprinids in the Upper Lake. The coregonid yield, 290 of 380 t total, comprised three-quarters of the landed catch during 1920–35 but has currently decreased to one quarter. Perch now prevail. *Salmo trutta*, *Esox lucius*, *Stizostedion lucioperca*, *Lota lota*, and *Anguilla anguilla* are other species of current economic interest but catches of the first three species are decreasing. In the Lower Lake, species composition in the harvest has remained unchanged during the review period. There, perch, cyprinids, two species of coregonids and northern pike are important contributors to the yield. The percentages of the total annual yields (kg/ha) from the two lakes before (1920–35) and after (1960–71) eutrophication that were contributed by the main components of the fishery were:

	Upper		*Lower*	
	Before	After	Before	After
Total yield	8	23	15	42
Coregonids	75	26	27	29
Cyprinids	12	24	43	44
Perch	9	48	13	15

Although yield has always been higher in the Lower than in the Upper Lake, the yield in each has tripled since the 1920–35 period. Increase in yield has been most rapid during the last 2 decades, when the tendency to eutrophy has been greatest (Nümann 1973).

Gear and Effort

During the 1920s an efficient anchored trap net (mesh size ⩾20 mm) was introduced into the Lake Constance fishery. Besides these trap nets, gill nets and different types of seines having mesh sizes ⩾30 mm were used. During the 1930s, most gill nets for perch had a mesh size of 30 mm. About 1959, the change from cotton to synthetic gill nets took place and the use of seines became much reduced. Although a minimum mesh size of 32 mm was prescribed for gill netting of perch, smaller meshes

TABLE 3. Mean annual standing crops of invertebrates and maxima of Tubificidae in the Upper and Lower lakes before and after eutrophication. Data on plankton are from Lehn (1972), those on benthos from Ritzi and Vogel (1959) and Zahner (1964).

Item	Years compared	Upper		Lower	
		Before	After	Before	After
Ciliata (n/ml)	54–70	3	11	3	21
Phytoplankton (n/ml)	35–70	240	1900	360	3400
Planktonic crustaceans ($n/m^2 \times 10^{-3}$)	28–62	20	260	80	380
Planktonic crustaceans (n/m^2)	54, 54	—	640	—	21600
Benthic crustaceans (n/m^2)	54, 55	—	8060	—	3200
Tubificidae (n/m^2)	54, 55	—	800	—	1000
$\text{Tubificidae}_{\text{max}}$ (n/m^2)	38, 54, 55 28, 59, 61	3000	177000	4450	10200

TABLE 4. Estimated fishing intensities by bottom gill nets in the Upper Lake in years representative of 1950–75.

Year	Number nets used[a]	Mesh size (mm)	Main fishing months	Nets licensed	Number of fishermen	Net material	Estimated fishing intensity factor
1951	1350	≥30	X–V	10	135[b]	cotton	0.05
1959	2300	32	X–V	18	129	cott./synth.	0.2
1967	3850	32	I–XII	21	180	synthetic	0.8
1974	4650	32	I–XII	27	173	synthetic	1.0

[a] The size of the nets (134 m^2) has not changed and no factor for different mesh size is used. The factor for cotton (Steinberg 1961) is 0.25. It is assumed that in the 1950s 50% of the fishermen that fished non-perch in the pelagial also fished with bottom gill nets in the littoral.

[b] Other estimations: 75 and much less.

are still used. During 1949–53, licenses for commercial fishing in the nearshore area totaled 75 for the Upper Lake and 110 for the Lower Lake. The number of licenses for sport-fishing was 1050 in the Upper Lake and 400 in the Lower Lake.

Once filleting became popular in the 1960s, perch became a desirable species and fishing intensity increased (Table 4). In spite of increasing effort and different management practices for perch and whitefish, yields were similar for the two species in terms of increase in landings and year-to-year fluctuations (Hartmann 1975). Currently in the Upper Lake, perch, pikeperch, and whitefish are probably overfished.

Eurasian Perch

Except as otherwise indicated, the following is from Nümann (1939, 1973) and Hartmann (1975).

Originally, the Eurasian perch in Lake Constance — as with many other German lakes — were subdivided into three types based upon coloration and distribution (Gaschott 1941). These differences are no longer apparent and coloration resembles that described by Scheffelt and Schweizer (1926).

Distribution, Food, and Feeding

Coincident with the progressive eutrophication of the lake, the depth chosen by the majority of adults increased (Hartmann and Löffler unpublished data). During winter, the depth chosen increased from 10 to 30 m in the 1930s to 40–50 m in 1976. During summer, distribution changed from littoral to sublittoral, 6–10 m. Currently, adults are caught in midwater, a previously unrecorded phenomenon. Population pressure, planktivory, and change of species composition of the fishes presumably caused the movement beyond the littoral areas.

This observed migration toward midlake has also occurred with other fish species in Lake Constance. Also, perch and/or cyprinids have changed distribution patterns in Lac Leman (Haempel 1930; Vivier 1975) and Lake Maggiore (Bonomi et al. 1970), apparently in response to eutrophication.

As might be deduced from changed distribution patterns, food preference has also changed coincident with eutrophication. The predominant food of perch during 1937–38, fish, has recently been replaced by *Daphnia* sp., *Bythotrephes* sp., and Chironomidae. Whitefish (*Coregonus lavaretus wartmanni*), burbot, and roach have similarly tended recently to select benthic and planktonic foods such that perch, roach, and whitefish now select similar food. Observed changes in food preference, however, have not decreased growth rates.

Nevertheless, although perch are becoming progressively more planktivorous, small perch still occur in the diet of adults. In addition to cannibalism by adult perch, northern pike and pikeperch also prey upon young perch. Young-of-the-year perch are also an important food item for eel (*Anguilla anguilla*) in summer (Quoss personal communication) and burbot (*Lota lota*) in winter.

Competition for plankton as food was observed among perch (*Perca fluviatilis*), whitefish (*Coregonus lavaretus wartmanni*), and roach (*Rutilus rutilus*). Sharing this food resource apparently had little effect upon growth as, even in a year when perch were extremely abundant, the other species grew extraordinarily well, in contrast to the period before eutrophication. Then, on the other hand, large stocks of whitefish grew slower than small stocks because of a limited plankton abundance. Other food sources are shared among fishes resident in Lake Constance but, because of abundant food resources, periodicity in feeding habits or differences in vertical or horizontal distribution, food does not appear to be limiting.

Yield

In the Upper Lake, annual yield has varied considerably (Fig. 2) and years of peak abundance appeared to coincide for whitefish (*Coregonus lavaretus wartmanni*) and perch (*P. fluviatilis*) once catch curves had been shifted so that birth dates of vulnerable stocks coincided.

The observed variations in yield appear to be caused mainly by temperature in association with predation. Within the last decade the years with the warmest growing seasons (1967, 1971, 1973) produced the richest year-classes of perch, whereas in the coolest summers (1968, 1972) poor year-classes occurred (Fig. 3). The quicker-growing fingerlings attained the upper size range of normal prey-fish earlier than slower growing fingerlings. Thus, the shift of many fishes to planktivory, coincident with lake eutrophication, meant an increased, but still limited, buffer effect of plankton against predators of the young perch of the year.

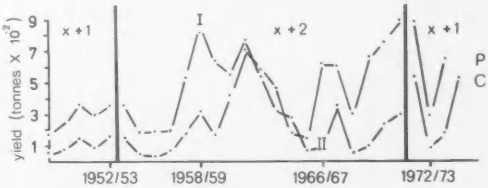

FIG. 2. Reported annual yields (tonnes) of Eurasian perch, *P. fluviatilis*, and whitefish, *Coregonus lavaretus wartmanni*, from Upper Lake Constance. The *Coregonus* yield curve (C) was shifted 1 (X + 1) or 2 (X + 2) intervals to the right. The years refer to the unshifted perch curve (P). Median of the intervals is January 1st. I, introduction of synthetic net material; II, catches prohibited for about 1 yr and rise of the prescribed mesh size from 40 to 44 mm. Shift of C curve takes into consideration that the whitefish is caught at an earlier age (I–III) than the perch (II–V).

Though the morphoedaphic index (Ryder et al. 1974) did not change, the average annual yield of perch increased during the period 1914–19 to 1967–74, from 28 to 779 t in the Upper Lake and from 20 to 139 t in the Lower Lake. The greatest increase in catches was from the shallow eastern part of the Upper Lake. Yield increased about 9 yr earlier (1958) in the Upper Lake (Nümann 1973). There was some evidence that increased effort in the Lower Lake may have caused the higher yields as quotas were removed in 1966 (H. O. Gaertner unpublished data).

These increased yields in the eutrophying lake may have resulted from: (i) increased abundance of benthos and plankton (Table 3) used as food, causing decreased cannibalism upon young-of-the-year perch (Hartmann 1975); (ii) more shelter and better spawning conditions resulting from increased vegetation (Nümann 1973); (iii) greater utilizable habitat from occupation of pelagic and littoral areas (Nümann 1973); (iv) reduced mean fish length resulting in reduced cannibalism (Hartmann 1975).

Growth and Age

Growth of perch and other species of the Upper Lake accelerated coincident with eutrophication. But the growth of perch in both parts of Lake Constance may, however, have been influenced more by fishing intensity than eutrophication. Fishing intensity increased from the 1930s to the present and appears reflected in the catch. In spite of the accelerated growth, lengths, and weights of catches made in 30-mm gill nets were lower after eutrophication than before even though cotton nets generally caught smaller fish than synthetic nets of the same mesh size (Hartmann 1975). These changes in size were also reflected by decreased catches in larger-mesh gill nets.

TABLE 5. Fish yields $kg^{-1} yr^{-1}$ of nine German or alpine lakes.

Lake	Year	Salmonids	Roach	Bream	Pikeperch	Perch
Alster	1950s	—	7	7	0.7	0.1
Schliersee[a]	1959	1	0.1	—		0.03
Hemmelsdorf	66/67	—	0.3	low	1	low
Pirk	61–63	—	37	17	0.6	0.3
Eder	65–73	?	?	?	3	0.7
Schaalsee	1949	3	ca 4	2	—	1
Lower	60–71	12	<14	<3	0.01	6
Leman[b]	60–74	?	?	?	—	10
Upper	60–71	6	<4	<1	0.05	11

[a] Morgenroth (personal communication) introduction of pikeperch 1957.

[b] Boyd and Laurent (personal communication).

Although perch may reach age 9, individuals near this age were rare in catches. Commercial catches were not consistently dominated by any age-group; between 1972 and 1976 the predominant ages of fish in the catches were 5, 2, 2, 3, 2, and 3 yr, respectively.

Generally, females spawn at 3 yr of age in the Lower Lake and at 2 yr in the Upper Lake. Before eutrophication, spawning lasted until mid-May; recently, it has been prolonged until late in May. This alteration in spawning season has also been observed with whitefish and burbot.

Diseases

Before eutrophication, mortality from disease periodically occurred during late summer, almost entirely in young-of-the-year perch. Causes were unknown. After eutrophication, there were early summer kills of adults apparently due to *Diplostomum* sp., which causes haematoma of internal organs. In 1966, nearly 50 t of perch were killed. From 1961 to 1971 Deufel (personal communication) reported large kills every 5 yr. Infestation of various fishes by parasites has generally increased following eutrophication and the increase in *Diplostomum* sp. has been attributed to the increase of vegetation and snails.

Pikeperch

Pikeperch were introduced into Lake Constance in 1882. Until recently, fingerlings were planted irregularly; from 1970 to 1974, the average annual stocking total was 45,000 (Strubelt personal communication). Stocking appears to be economically unfeasible as yield only approximates rearing costs.

In the Upper Lake, reported annual yields of pikeperch increased from 1 t in the 1920s to 11 t in the 1950s and decreased to 2 t in the 1970s. The irregular year-to-year yields in no way reflect the related parallel changes in yields (Fig. 2) of perch and whitefish.

Several factors, however, may compound the lack of apparent regularity in yield. A large proportion of the yield was unreported and significant catches of juveniles, below the legal size limit of 40 cm, were made in eel traps and 32-mm gill nets.

Growth data collected before eutrophication (Haakh 1929) indicate that growth has recently accelerated.

Growth of pikeperch in Lake Constance is good according to the classification of Tesch (1961) and appears similar to that in other subalpine lakes (Schmid 1972). But, compared with northern Germany (Hagena 1969) yield of pikeperch in southern Germany, including Lake Constance, is low. Only moderate stocking success of pikeperch by introduction has been found elsewhere (Tesch 1961).

Comparisons with Lake Constance to Other Lakes

Following eutrophication, perch in Lake Constance grew better than those in most other German unpolluted lakes except the Laacher See population (Haakh 1929). However, yields (Table 5) in the Upper Lake, 0.6 kg/ha, and the Lower Lake, 3.0 kg/ha, before eutrophication were similar to those of many northern German lakes (Dröscher 1908; Laskar 1945; Tesch 1955). On the other hand, yields in the Upper and Lower Lakes after eutrophication, 16 and 12 kg/ha, respectively, were not attained by any other German lake (Table 5). Usually, high yield in northern German lakes was associated with moderate growth by perch, and medium or low yield with very good or good growth (Tesch 1955). In Lake Constance, however, high yield now occurs (Fig. 2) in association with very good growth.

In central Europe, perch generally comprise about 8% of the landed catch (Wundsch 1973).

In Lake Constance, however, perch account for approximately 48% of the catch (Table 5). Though the percentage of perch in the catches has been high elsewhere, e.g. 58% of the yield from Lac Léman (Boyd and Laurent personal communication), it is unusual.

In many German lakes the classic ontogenetic succession in food is observed, i.e. plankton to benthos to fish. But after eutrophication in the Upper Lake, the main food of perch appears to have been invertebrates with the unusual seasonal change from plankton to benthos. Tesch (1955) concluded that availability of fish or decapods for food was necessary for normal growth and yield in northern German lakes, but in Lake Constance invertebrate feeding appears quite adequate.

In Lake Constance, few perch older than age 5 were found, as in other German lakes (Tesch 1955). Spawning by females at 2 yr of age has also been reported in northern German lakes. However, no correlation appears to exist between growth rate and age at maturation as spawning at age 2 has occurred in populations having high growth rates as well as those having considerably poorer growth (Tesch 1955).

Regular perch kills after spawning as observed in Lake Constance after eutrophication have been reported from other German lakes, too.

From 17 case histories of European lakes undergoing eutrophication (Hartmann 1977), four stages of fish yield succession can be distinguished. Both basins of Lake Constance belong to the first stage, which is characterized by an increasing or at least not decreasing yield of coregonids and increasing yields of percids and cyprinids. Usually, with greater eutrophication perch yield decreases and in 7 out of 10 cases, including both basins of Lake Constance, perch and pikeperch yields developed divergently. These observations correspond to the statement of Tesch (1955) that perch yield is highest in coregonid lakes beginning to eutrophy.

In Lake Constance the relationship between coregonid and perch yields were variable. Both a negative (Nümann 1973) or positive (Hartmann 1975) correlation was found between perch and coregonine yields. Probably oxygen deficits in profundal areas cause greatest negative effects on coregonids whereas the marginal lake regions — the main perch habitat — do not suffer as significant deleterious effects.

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Effects of Exploitation, Introductions, and Eutrophication on Percids in Lake Balaton[1]

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BIRÓ, P. 1977. Effects of exploitation, introductions, and eutrophication on percids in Lake Balaton. J. Fish. Res. Board Can. 34: 1678–1683.

Percid populations in Lake Balaton have undergone changes which are considered to have been caused by individual or combined effects of overfishing, interspecific competition from nonnative species, and loadings of nutrients and pesticides. Eurasian perch (*Perca fluviatilis*) has almost disappeared and the ruffe (*Gymnocephalus cernua*) population is declining, probably as a result of competition from the eel (*Anguilla anguilla*) and effects of cultural eutrophication. Growth rate of pikeperch (*Stizostedion lucioperca*) is declining while that of the bream (*Abramis brama*) is increasing. Production of cyprinids has increased up to 10% in recent years, apparently in response to accelerated eutrophication. The exploitation rate of pikeperch is far in excess of that considered necessary for maximum sustained yield. The environment in the most eutrophic part of the lake is now considered to be unfavourable for pikeperch.

Key words: Percidae, *Stizostedion*, *Perca*, *Gymnocephalus*, exploitation, eutrophication, introductions, ruffe, Lake Balaton

BIRÓ, P. 1977. Effects of exploitation, introductions, and eutrophication on percids in Lake Balaton. J. Fish. Res. Board Can. 34: 1678–1683.

Les populations de percidés du lac Balaton ont subi des changements que l'on croit causés par les effets individuels ou combinés de la surexploitation, de la concurrence interspécifique d'espèces non indigènes et des charges d'éléments nutritifs et de pesticides. La perche eurasienne (*Perca fluviatilis*) a presque entièrement disparu, et la population de perches goujonnières (*Gymnocephalus cernua*) diminue, probablement par suite de la concurrence de l'anguille (*Anguilla anguilla*) et des effets de l'eutrophisation agricole. Le rythme de croissance du doré bleu (*Stizostedion lucioperca*) diminue, alors que celui de la brème (*Abramis brama*) augmente. La production de cyprinidés accuse en ces dernières années des augmentations allant jusqu'à 10%, apparamment en réponse à une eutrophisation accélérée. Le taux d'exploitation du doré bleu excède de beaucoup ce qui est considéré comme nécessaire au rendement maximum soutenu. L'environnement dans la partie la plus eutrophe du lac est considéré comme étant défavorable au doré bleu.

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THE purpose of this paper is to describe changes in percid populations in Lake Balaton with particular reference to effects of exploitation, introductions, and eutrophication. The percid community consists of the predominant pikeperch (*Stizostedion lucioperca*), the Volga pikeperch (*S. volgensis*) and the ruffe (*Gymnocephalus cernua*). Eurasian perch (*Perca fluviatilis*) is now very rare.

Lake Balaton (46°50′N, 17°40′E) is the largest shallow (<12 m) lake in central Europe (Fig. 1). The environment of the lake has changed considerably since 1945. Accelerated cultural eutrophication, especially since 1965, resulted in deteriorated water quality and changes in the biota over extensive parts of the lake.

The present analysis of changes in the Lake Balaton percid community is based mainly on commercial catch statistics. Information on population dynamics, predator–prey relations, and energy transformations in percids has been presented in Biró (1970, 1971, 1972, 1973, 1975).

Limnology

Despite a large surface area, the volume of Lake Balaton is small because of its shallow depth (Table 1). The littoral area (depth to 1.5 m) is approxi-

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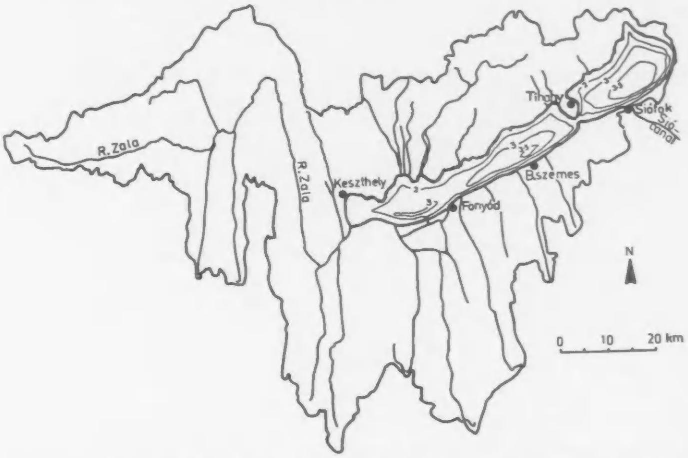

FIG. 1. Lake Balaton and its catchment area (modified from Vituki 1953). Isobaths in metres.

TABLE 1. Morphometry and selected physicochemical data ($mg \cdot \ell^{-1}$ except as indicated) of Lake Balaton.

Variable	Value	Variable	Value
Catchment area (km^2)	5774	Sodium	26.5–53.0
Lake surface (km^2)	596	Sulphate	12.9–13.2
Altitude (m)	104	Hydrogen carbonate	281–287
Annual fluctuation, mean (cm)	55	Ammonium	0.09–0.27
Length (km)	77	Nitrite	0.005
Width (km)	1.5–15	Nitrate	0.1–0.6
Depth, mean (m)	3	Total N	3
Depth, maximum (m)	11.2	Phosphate	0.0–0.02
Volume (km^3)	1.8	Total P	0.05
Inflow, mean ($m^3 \cdot s^{-1}$)	16.9	Silicon	4.6–17.8
Outflow, mean ($m^3 \cdot s^{-1}$)	11.7	Conductivity (20°C) ($\mu s \cdot cm^{-1}$)	409–471
Precipitation ($m^3 \cdot s^{-1}$)	12	pH	7.85–8.78
Evaporation ($m^3 \cdot s^{-1}$)	17.2	Transparency (Secchi disc) (cm)	50–70
Catchment area/lake area	9.69	Suspended matter	6.0–20.4
Catchment area/lake volume	3208	Total dissolved solids	400
Shoreline length/lake volume	108	Alkalinity ($CaCO_3$) (meq)	4.6–4.7
Shoreline development factor	2.25	DO (% saturation)	20–198
Turnover time (yr)	2.2	BOD	4.5–6.2
Period of ice-cover	Dec.–Feb.	Eh (mud interface) (mV)	300–400
Deposits from streams ($t \cdot yr^{-1}$)	79,300	Organic C (in mud) (%)	1.5–1.8
Deposited dust ($t \cdot km^{-2} \cdot yr^{-1}$)	47	Chlorophyll *a* ($\mu g \cdot cm^{-2}$)	2.9–15.5
Sedimentation rate ($mm \cdot yr^{-1}$)	0.35–0.8	Bacterial production ($t \cdot ha^{-1} \cdot yr^{-1}$)	4.7
Calcium	31.8–34.2	Phytoplankton production ($t \cdot ha^{-1} \cdot yr^{-1}$)	14.1
Magnesium	42.3–44.3	MEI	133.3

mately 100 km^2. An area of 8 km^2 (25% of the shoreline) is covered by *Phragmites* sp. (Muszkalay 1973).

Human population in the catchment area is about 123,000 with increases during the tourist season. There are 6 large and about 900 minor sewage outfalls within the catchment area with an estimated flow of 74,000 $m^3 \cdot yr^{-1}$ (Muszkalay 1973).

Mean annual water temperature is about 10°C; summer temperature varies between 21.7 and 24.7°C (Kessler 1974). The lake does not stratify thermally. Ice-cover (mean duration — 44 days) averages 25 cm in thickness (maximum — 72 cm). On the basis of water chemistry, the lake can be divided into northern, middle, and southern sections. Sodium salts are higher in the northern part, but the southern section is the most polluted area in the lake. The water is usually well saturated with oxygen (Entz 1953) and because of mineralization its buffering capacity is high (Oláh 1971).

The northern and central parts of the lake are mesotrophic to eutrophic and the southern part is highly eutrophic. Primary production varies from about 100 g C $m^{-2} \cdot yr^{-1}$ in the north to over 800 g C $m^{-2} \cdot yr^{-1}$ in the south (Herodek and Tamás 1975). In recent years, blue-green blooms (*Aphanizomenon* sp. and *Microcystis* sp.) have been the predominant algae in several areas. Recent increases in epiphytic and epibenthic algae also indicate increasing eutrophy. The littoral and supralittoral areas are covered by *Bangia* sp., *Cladophora* sp., and *Ulothrix* sp. (Tamás 1974a, b). Continuous stands of *Phragmites* sp. border the northeastern shoreline. In open water *Potamogeton perfoliatus* and *Myriophyllum spicatum* are predominant (Kárpáti 1974). In recent years scattered stands of *Elodea canadensis* and *Stratiotes aloides* appeared throughout the lake, providing further evidence of rapid eutrophication (Tóth 1972).

Limnomysis benedeni and *Dreissena polymorpha* are common detritus feeders (Woynárovich 1955). The mud in the southern part is densely populated with chironomids (*Chironomus ex. gr. plumosus*, *Tanypus punctipennis*, and *Procladius* sp.).

There are 40 species of fish indigenous to Lake Balaton and its tributaries. Cyprinidae (23 spp.) and Percidae (6 spp.) are predominant. Twelve of the cyprinid species and three of the percids are common. About 15 species have economic importance.

History of the Fisheries

Relics from early settlements indicate that Lake Balaton has been fished by man since 5000 B.C. (Sági 1974). The first records (A.D. 1008) of fishing rights indicate that these were granted to religious orders by the monarchy. Information dated 1230 showed that seines and gill nets were used (Hankó 1931). There are several records (Herman 1887) of the richness of the fishery up to the Turkish occupation in the 16th century. During the Turkish rule (150 yr) the fish stocks in Lake Balaton declined. Flood control projects in the 19th century further affected the fishery throughout water level fluctuation and elimination of important spawning areas. During the same period fishing pressure was increasing; in 1880 the number of gill nets was estimated at 20,000.

Effective regulations were introduced in 1884 with the establishment of the Balaton Fishing Co-operatives (Répássy 1909). The Balaton Fishing Corporation, founded in 1900, rented the entire lake for fishing for 50 yr. The corporation improved the fishery through stocking, collection of fishery data, protection of spawning pikeperch, and modernization of gear. In the 1900–13 period the annual average catch was 12.5 $kg \cdot ha^{-1}$ (750 t). From 1926 to 1940 the annual average catch was 19.7 $kg \cdot ha^{-1}$ (1200 t). The pikeperch harvest doubled from the previous period to 160 t and the carp (*Cyprinus carpio*) catch increased from 8.5 to 50 t.

In 1948 the fisheries of Lake Balaton were taken over by the state (Woynárovich 1958). Because of increased fishing pressure, annual harvests first increased and then decreased. Pikeperch harvest dropped to 120 t annually. In July 1975 the management of the fisheries came under the authority of the Ministry of Food and Agriculture.

Exploitation

Between 1902 and 1973 the annual commercial fish yield varied between 300 and 1963 t or 5 and 33 $kg \cdot ha^{-1}$ (Fig. 2). Pikeperch amounted to 6–12% of the total catch during the 1950–73 period in comparison with about 78% for bream (*Abramas brama*). Distribution of the catch varied in the lake with 37% coming from the southeastern basin in 1973 (Fig. 3). Following a massive fish kill in 1965 the yearly catch of pikeperch dropped to one-third of the 1950–64 average but has since returned to prior levels.

Between 1964 and 1973 about 1.6–4.8 pikeperch ha^{-1} were harvested annually from the standing crop which had been assessed as 10.5–20.3 ha^{-1} (Biró 1975). On the basis of a 65% average annual mortality (Biró 1975), the biomass loss was between 255.7 and 495.9 t (4.3 and 8.3 $kg \cdot ha^{-1}$). The commercial fishery removed between 60 and 180 $t \cdot yr^{-1}$ (1–3 $kg \cdot ha^{-1}$) or 24–36% of total production. The remaining 20–41% was due to the sport fishery and natural mortality.

The instantaneous natural mortality coefficient ($M = 0.373$) has been estimated for pikeperch from 1964 to 1973 data. Hence the instantaneous fishing mortality coefficient at the fixed level was $F = 0.67$. The rate of exploitation, estimated by the method of Cushing (1968), was 41%. In addition to the mortality coefficients (M and F), the growth parameters for pikeperch ($K = 0.1376$, $L_\infty = 75.7$ cm, $t_0 = -0.91$ yr, $W_\infty = 6.429$ g) and maximum age ($\lambda = 15$ yr) were used for yield-per-recruit estimates (Beverton and Holt 1957). Recruitment was assumed to be $R = 1$.

Although the proportion of age-groups 1+ and 2+ together amounts to only 8% of the population, the exploitation of catchable pikeperch starts with age-group 2+. The fishable life span of pikeperch is 13 yr, but individuals older than 9+ are few and relatively unimportant. Age-groups 3+ to 6+ are most significant in the fishery. Their yield increases only to a small extent as fishing mortality surpasses the fixed point of $F = 0.67$ (Fig. 4). As a result of the relatively high natural mortality, the yield-per-recruit curves do not show the classical peaked form. Modification of F is followed by increased or decreased yield according to the age of the fish.

Biomass of pikeperch proportional to catch per

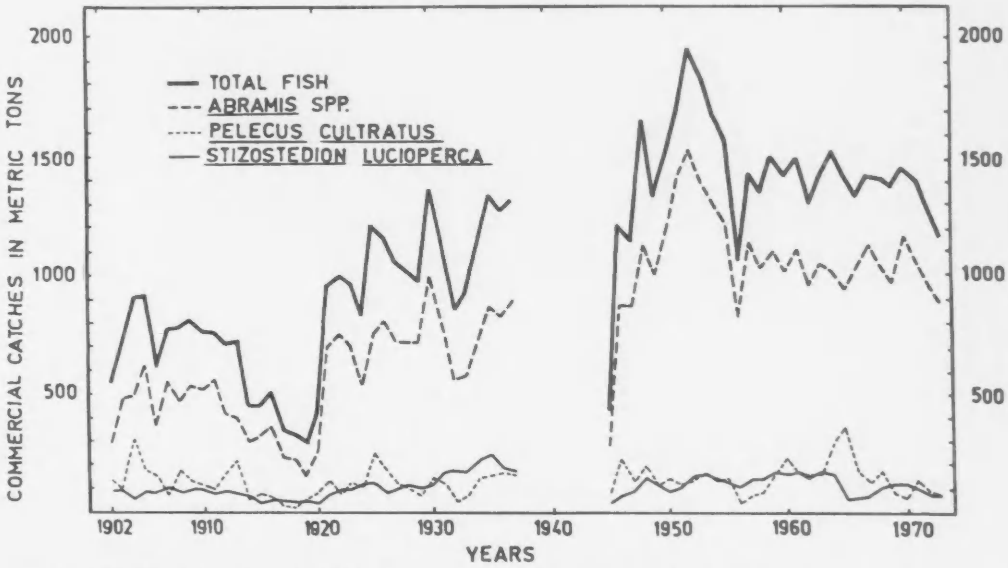

FIG. 2. Commercial catches of all fish, *Abramis* spp., siege (*Pelecus cultratus*), and pikeperch (*Stizostedion lucioperca*) in Lake Balaton, 1902–73.

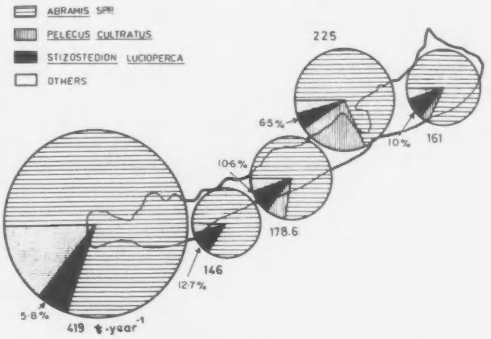

FIG. 3. Total commercial landings ($t \cdot yr^{-1}$) and percentage compositions of important species for several areas of Lake Balaton, 1972–73.

unit effort (CPE) varies inversely with fishing mortality (*F*). In the fishable age-groups a significant decrease of CPE is likely to follow an enlargement of *F* (Fig. 5). The point *H* on the yield isopleths (Fig. 6) indicates the present level of exploitation of the pikeperch populations. It occurs at the intersection of the fixed level of fishing intensity ($F = 0.67$) for the 1964–73 period and the age at first capture ($t_c = 2.9$ yr). The locus of maximum sustainable yield (MSY), the level of exploitation at which the harvested pikeperch population should be maintained to produce maximum yield, ranges between 9 and 12 yr which is an indication of the extent of overfishing of the present population. MSY could be obtained at a fairly high age at first capture.

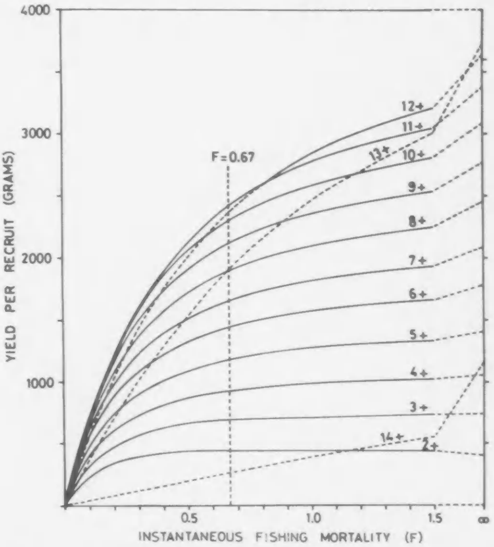

FIG. 4. Relations between equilibrium yields and fishing mortalities for various age-groups of pikeperch in Lake Balaton, 1964–73.

Selected sections through the yield isopleths

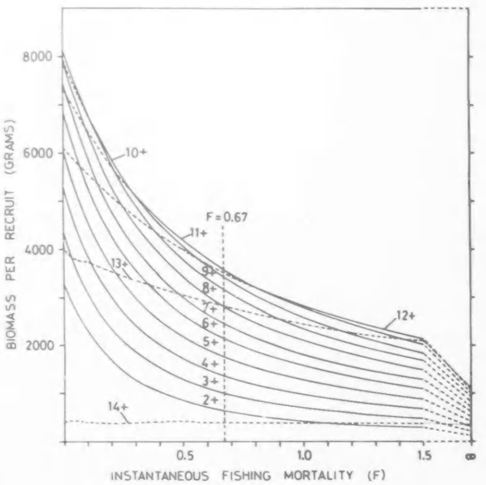

FIG. 5. Relations between biomass per recruit (assumed to be proportional to catch per unit effort) and fishing mortalities for various age-groups of pikeperch in Lake Balaton, 1964–73.

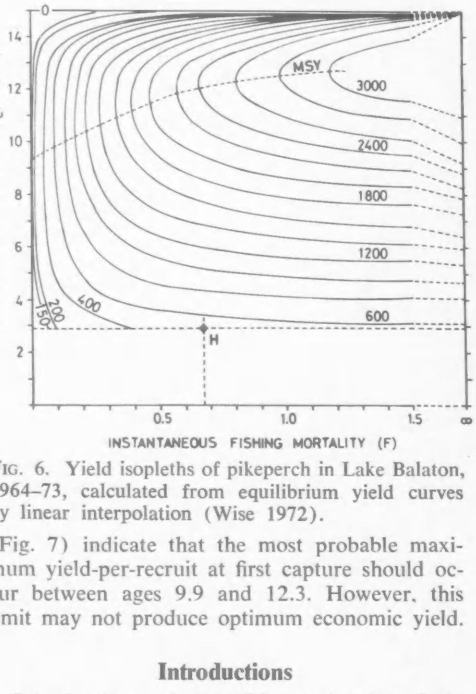

FIG. 6. Yield isopleths of pikeperch in Lake Balaton, 1964–73, calculated from equilibrium yield curves by linear interpolation (Wise 1972).

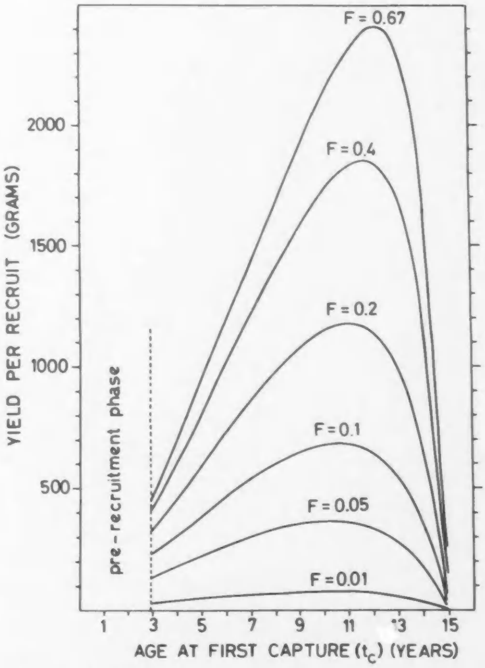

FIG. 7. Relations between yield per recruit and age at first capture for pikeperch in Lake Balaton, selected from data in Fig. 6.

(Fig. 7) indicate that the most probable maximum yield-per-recruit at first capture should occur between ages 9.9 and 12.3. However, this limit may not produce optimum economic yield.

Introductions

Introductions of new fish species into Lake Balaton and its tributaries started early in this century. Catfish (*Ictalurus nebulosus*) and largemouth bass (*Micropterus salmoides*) of North American origin became acclimatized but reproduced poorly. Pumpkinseed (*Lepomis gibbosus*) now inhabit the littoral zone. Stocking of carp has occurred since 1925 to reduce (unsuccessfully) the dense bream population. After 1945 the annual catch of carp dropped from 50 to 25 t. Vendace (*Coregonus albula*), stocked in the 1950s to exploit offshore zooplankton (Ribiánszky and Woynárovich 1962), was unable to withstand high summer temperatures (20–25°C). *Neogobius fluviatilis* appeared in Lake Balaton in 1970. *Pseudorasbora parva* and *Ctenopharyngodon idella* entered the lake from nearby ponds. Other introductions included *Hypophthalmichthys molitrix* and *H. nobilis*. All of these plantings did not result in a significant increase in the fish yield of Lake Balaton.

The eel (*Anguilla anguilla*) was introduced as early as 1890 (Vásárhelyi 1962) and large plantings were made in the 1960s. The eel became very abundant in some inshore areas and undoubtedly caused an increase in interspecific competition. Following the plantings in the 1960s the crayfish (*Astacus leptodactylus*) disappeared. During 1965–68 Eurasian perch almost disappeared. Also there were declines in the stock of ruffe and bleak (*Alburnus alburnus*) which may be partly due to the eel (Biró 1973).

Eutrophication

Water quality began to deteriorate at the beginning of this century with modifications in shoreline and water levels. The loss of marshes gradually affected several species of fauna and flora. The pikeperch lost original spawning grounds and a food source for fry.

As a consequence of progressive human development and increased nutrient loadings from sewage and agriculture, the initial obvious signs of eutrophication appeared in the 1930s. In the 1950s there was a sudden increase in the use of artificial fertilizers and pesticides (Sebestyén 1967). In 1965 pesticides were implicated in a kill of 500 t of fish (40% pikeperch). Local fish kills (70 t) in the spring of 1975 may have been caused by intensive algal blooms. Between 1961 and 1973 productivity of algae in Keszthely Bay increased eightfold and the basin is now considered to be hypereutrophic (Herodek and Tamás 1975).

During recent years the productivity of valueless fish has increased by some 5–10% in the most eutrophic areas, especially Keszthely Bay. Some of the more sensitive fish species have declined, thus enabling the bream to utilize the vacated areas more effectively for spawning and feeding. Eurasian perch has almost disappeared and the stock of ruffe is declining, although the eel may have been a factor in these changes. Growth rate of the pikeperch declined from that of the 1930s (Unger 1931) while the bream grew faster due to changed environmental conditions (Biró and Garádi 1974). It is evident that cultural eutrophication does not ultimately create favorable conditions for pikeperch.

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A Review of Pikeperch (*Stizostedion lucioperca*), Eurasian Perch (*Perca fluviatilis*), and Ruff (*Gymnocephalus cernua*) in Finland[1]

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LIND, E. A. 1977. A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*) in Finland. J. Fish. Res. Board Can. 34: 1684–1695.

Three percids occur in Finland: the Eurasian perch (*Perca fluviatilis*), the pikeperch (*Stizostedion lucioperca*), and the ruff (*Gymnocephalus cernua*). Perch occur throughout Finland, whereas ruff and pikeperch show a more southerly distribution. The pikeperch prefers lakes of medium or large area and the perch small lakes. A negative correlation was found between the size of the population of the perch and the number of fish species present. The growth rate for all species is higher in brackish water than in freshwater, and also has been higher in recent than earlier years.

The correlation between the intensity of color of the water and the percentage of predaceous fish in catches, perch and pikeperch included, is negative. Perch lived longer in ponds with dark water than in those with clear and eutrophic waters. Ruff and small perch are typically prey species, while the pikeperch is a major predator.

The environmental toxins cadmium, lead, DDT, and PCBs were found in only slight concentrations in percids. Highest concentrations of mercury were found in fish taken from waters near the main sites of the cellulose industry. Concentrations in the percids have decreased since 1968 due to the reduction in mercury output.

Catches of pikeperch from freshwater showed a decrease and those from brackish water an increase during 1953–73. Perch catches have increased.

Key words: Percidae, Finnish percids, *Stizostedion*, *Perca*, *Gymnocephalus*, life history, environmental toxins, heavy metals, distribution, water color, yield

LIND, E. A. 1977. A review of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*) in Finland. J. Fish. Res. Board Can. 34: 1684–1695.

Trois percidés se rencontrent en Finlande: la perche eurasienne (*Perca fluviatilis*), le sandre (*Stizostedion lucioperca*) et la perche goujonnière (*Gymnocephalus cernua*). La perche eurasienne est répartie dans toute la Finlande, alors que la perche goujonnière et le sandre ont une répartition plus méridionale. Le sandre préfère des lacs de superficie moyenne ou grande, et la perche eurasienne des lacs plus petits. Nous avons trouvé une corrélation négative entre la taille de la population de perches eurasiennes et le nombre d'espèces de poissons présentes. Le rythme de croissance de toutes les espèces est plus élevé en eau saumâtre qu'en eau douce et a été plus rapide récemment que durant les années antérieures.

La corrélation est négative entre l'intensité de la couleur de l'eau et le pourcentage de poissons prédateurs dans les prises, y compris la perche eurasienne et le sandre. La perche eurasienne vit plus longtemps dans des étangs d'eau foncée que dans des étangs clairs et eutrophes. Le sandre et les petites perches eurasiennes sont typiquement des espèces proies, alors que le sandre est un prédateur majeur.

Les substances toxiques du milieu, le cadmium, le plomb, le DDT et les BPC ne se trouvent qu'en faibles concentrations dans les percidés. Les concentrations maximales de mercure se trouvent dans les poissons capturés à proximité des principaux sites de l'industrie de la cellulose. Les concentrations dans les percidés diminuent depuis 1968 par suite de la diminution des sorties de mercure.

Entre 1953–73, les prises de sandres diminuèrent en eau douce et augmentèrent en eau saumâtre. Les prises de perches eurasiennes augmentèrent.

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THE purpose of this paper is to review investigations into percid fishes in Finland, the majority of which have been published in Finnish only.

Both fresh and brackish waters in Finland are inhabited by three percid species: pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and ruff (*Gymnocephalus cernua*). Early studies were on age, size, food, and exploitation of these species. Since 1960 the structures and densities of perch and ruff populations have been studied in ponds, rivers, and lakes. Mortality rates and data on movement have been obtained from tagging studies for pikeperch and perch.

Reliable catch statistics have been published since 1953 by the Finnish Game and Fisheries Research Institute, Fisheries Division, for pikeperch and perch, and catch data for ruff have been collected in some lakes and brackish-water areas. During 1966–76 the presence of heavy metals and some other contaminants in fish was monitored.

Description of Percid Waters

Freshwater in Finland amounts to about 32,000 km^2, and the major brackish-water areas, the Gulf of Finland and the Gulf of Bothnia, to about 29,500 km^2 and 117,000 km^2, respectively. Areas where percid studies have been carried out are identified in Fig. 1. Limnological data on a number of lakes, rivers, and brackish-water areas are given in Table 1.

Climatic conditions vary considerably in different parts of the country due to latitude, and differences in altitude also produce marked fluctuations in weather. These differences are illustrated by the length of time for which the waterways are frozen which ranges from 3 to 9 mo. The freezing process is delayed in deep lakes in southern Finland and in brackish-water areas. The growing season lasts for about 170 days in the southern part of the country and for scarcely 100 days in the north.

Most of the 55,000 lakes are shallow with very irregular shorelines. Their mean depth is about 7 m and the total length of their shorelines is more than 130,000 km. The rivers are usually short and many of them have been dammed for hydroelectric power.

Many of the lakes and rivers drain wet peatlands, and consequently the water is sometimes strongly colored by humic colloids. As a result, most of the lakes in central Finland belong to the dystrophic type, whereas those in the southwestern part of the country are eutrophic (Fig. 2). Oligotrophic lakes occur in the southeast and north.

In recent years the increased use of fertilizers in agriculture and forestry has resulted in some eutrophication, and a number of lakes in the midst of extensive arable areas have become eutrophic since 1950.

A number of rivers, small lakes, and brackish-water areas, mostly in southwestern Finland, have been classified as polluted or unclean, though the majority of the fresh- and brackish-water areas are considered unchanged. The highest concentrations of mercury were found in fish from the main sites of the cellulose industry regions, the watercourses of Kymijoki, Kokemäenjoki, and Oulujoki.

The number of licensed fishermen in the freshwater area is 300,000, or about 10 ha/license, and in the brackish-water area 175,000, or 40 ha/license.

Distribution

All three percid species populate both fresh- and brackish waters. The perch occurs throughout Finland, but the ruff and pikeperch are absent from the northernmost districts (Fig. 3 and 4). However, the greatest concentration of percids (especially pikeperch) is in the lakes and brackish-water areas of the southern parts of the country.

Distribution of the percids is probably related to their spawning time and spawning-temperature requirements. The perch, which spawns from the beginning of May to the beginning of June (Kukko et al. 1972b; Lind et al. 1973a, b), occurs in northern Finland. The pikeperch, which usually spawns in June in southern Finland and at the end of June or beginning of July at the northern end of its range (Brofeldt 1961), shows a more southerly distribution pattern. Possibly the shortness of the summer in northern latitudes is a limiting factor in the distribution of the pikeperch. Also, pikeperch prefers dark waters, and most of the lakes in northern Finland are oligotrophic.

Pikeperch and perch are relatively more abundant in freshwater than in brackish water (Table 2). There is a negative correlation between the populations of plankton feeders and the intensity of color of the water, whereas the correlation between the predators and the intensity of color of the water is positive (Fig. 5). These correlations result in a negative correlation between the yield and the intensity of color of the water. Perch prefers small lakes and ponds (Fig. 6). Pikeperch occurs only occasionally in lakes <50 ha, while ruff shows no preference for lake size.

Catch Statistics

Most fish are caught in the period May–June, the principal spawning months for the percid species. However, low catches of pikeperch in June are due to the closed season because of spawning. During 1944–46, when pikeperch was fished throughout the year, the catch figures showed one peak in June (Hurme 1959).

In Kiutajärvi, where perch was caught throughout the year, most fish were obtained during June–September, when the catches amounted to about 50 individuals/day, whereas the usual num-

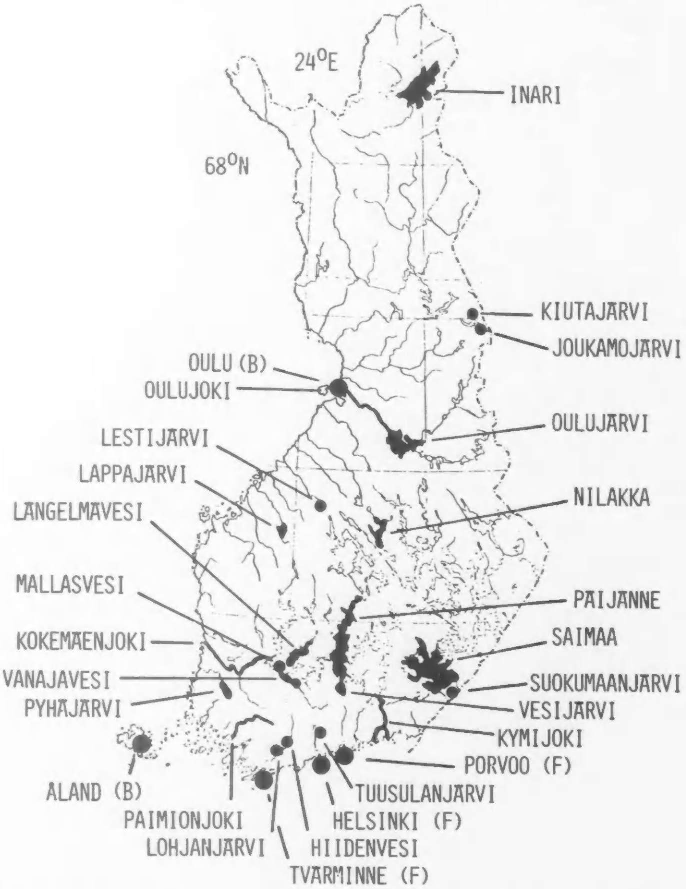
24°E
68°N
INARI
KIUTAJÄRVI
JOUKAMOJÄRVI
OULU (B)
OULUJOKI
OULUJÄRVI
LESTIJÄRVI
LAPPAJÄRVI
LÄNGELMÄVESI
NILAKKA
MALLASVESI
PÄIJÄNNE
SAIMAA
KOKEMÄENJOKI
VANAJAVESI
SUOKUMAANJÄRVI
PYHÄJÄRVI
VESIJÄRVI
KYMIJOKI
PORVOO (F)
ÅLAND (B)
TUUSULANJÄRVI
PAIMIONJOKI
HELSINKI (F)
LOHJANJÄRVI
HIIDENVESI
TVÄRMINNE (F)

FIG. 1. Lakes, rivers, and brackish-water areas from which data on the percid fishes are available. Small dots, small lakes; large dots, sites in brackish-water areas. The ponds are not included here.

ber of fish caught in winter was about 2/day (Lind et al. 1973a).

The catch of pikeperch in 1959 (Heikkinen 1960) was 253 t from brackish water and 739 t from freshwater, the most productive areas being in the south (Fig. 3). Average yield from freshwater was 0.3 $kg \cdot ha^{-1}$. Corresponding data for perch (Fig. 4) were 1896 t for brackish water and 3643 t for freshwater, the most productive areas being in the eastern and southern parts of Finland. Average yield of perch in freshwater was 1.3 $kg \cdot ha^{-1}$.

Some marked trends may be noted in the catches of the pikeperch during 1953–73 (Liedes 1954; Heikkinen 1960; Finnish Fish and Game Research Institute, Fisheries Division 1974, 1976; Suomen Kalastuslehti 1976). The catches from brackish water increased from about 200 t to about 700 t, whereas those from freshwater decreased from about 1400 to 300 t. The catches of the perch from brackish water increased from 1700 to 2700 t, and those from freshwater increased from 3100 to 5900 t. As a result, the total catch of perch increased from 4900 to 8600 t.

Growth Rate

The average growth rate is higher in brackish-water areas than in freshwater areas for all three percid species, apparently as a result of a greater food supply in brackish water (Fig. 7). However, pikeperch in brackish water are smaller at the age of 1 yr, possibly because spawning

TABLE 1. Limnological data from typical lakes, rivers, and brackish-water areas. Most samples were analyzed in the winters of 1968–73.

	Altitude (m)	Area (km²)	Max. depth (m)	Conductivity (μS·cm⁻¹)	Color (Pt mg·ℓ⁻¹)	pH	O_2 (mg·ℓ⁻¹)
Lakes							
Hiidenvesi	33	28.7	30	65	63	6.7	11.7
Tuusulanjärvi	38	6.3	10	178	63	6.5	0.6
Pyhäjärvi	44	155.0	25	69	15	6.9	11.7
Lappajärvi	69	140.0	30	41	55	6.7	12.3
Längelmävesi	84	224.0	>20	44	20	6.7	11.6
Vesijärvi	81	146.7	35	116	10	6.8	8.5
Lohjanjärvi	32	30.9	58	95	80	6.7	10.7
Nilakka	102	161.7	18	33	40	6.6	11.1
Saimsa	76	1460.0	82	34	45	6.7	12.6
Kiutajärvi	225	0.5	24	51	25	7.4	10.6
Inari	119	1085.0	95	29	15	7.1	12.9
Mallasvesi	84	64.0	>20	59	15	6.6	12.2
Vanajavesi	80		23	89	80	6.7	7.9
Lestijärvi	140	64.9	10	26	70	6.0	11.3
Joukamojärvi	252	23.9	>13	40	20	6.6	8.5
Oulujärvi	123	900.0	35	28	60	6.3	11.7
Rivers							
Kokemäenjoki, Rautavesi	42	30.0	40	98	65	6.1	4.1
" Liekovesi	42	4.5	>5	98	65	6.1	4.1
Paimionjoki			>3	123	90	7.2	11.7
Brackish-water areas							
Gulf of Finland, Porvoo		29500.0	116	9000	15	7.4	10.5
" Helsinki				7700	20	7.6	11.2
Gulf of Bothnia, Oulu		117000.0	291	4300	30	7.1	11.8

TABLE 2. Annual catches of various fish species obtained from brackish-water and freshwater areas in Finland in 1973. Data from Finnish Game and Fisheries Research Institute, Fisheries Division (1974).

	Brackish-water areas		Fresh-water areas		Total	
	(t)	(%)	(t)	(%)	(t)	(%)
Clupea harengus (Pl.)	67,071	83.3			67,071	68.9
Perca fluviatilis (Be. Pr.)	2,291	2.8	4,374	26.2	6,665	6.8
Esox lucius (Pr.)	1,674	2.1	3,452	20.7	5,126	5.3
Coregonus albula (Pl.)	1,180	1.5	3,546	21.2	4,726	4.9
Coregonus sp. (Be.)	1,986	2.5	828	5.0	2,814	2.9
Abramis brama (Be.)	985	1.2	1,160	7.0	2,145	2.2
Clupea sprattus (Pl.)	1,854	2.3			1,854	1.9
Lota lota (Pr.)	650	0.8	1,155	6.9	1,805	1.9
Stizostedion lucioperca (Pr.)	628	0.7	435	2.6	1,063	1.1
Salmo sp. (Pr.)	640	0.7	137	0.8	777	0.9
Osmerus eperlanus (Pl.)	442	0.5	102	0.6	544	0.6
Leuciscus idus (Be.)	210	0.2	196	1.2	406	0.4
Gadus morhua (Pr.)	95	0.1			95	0.1
Miscellaneous	932	1.1	1,284	7.7	2,216	2.2
Plankton feeders (Pl.)	70,547	87.5	3,648	21.9	74,195	76.3
Benthos feeders (Be.)	4,326	5.4	4,371	26.2	8,697	8.9
Predators (Pr.)	4,833	6.0	7,366	44.2	12,199	12.5
Miscellaneous	932	1.1	1,284	7.7	2,216	2.3
Total	80,638	100.0	16,669	100.0	97,307	100.0
kg·ha⁻¹	11.0		5.2		9.2	

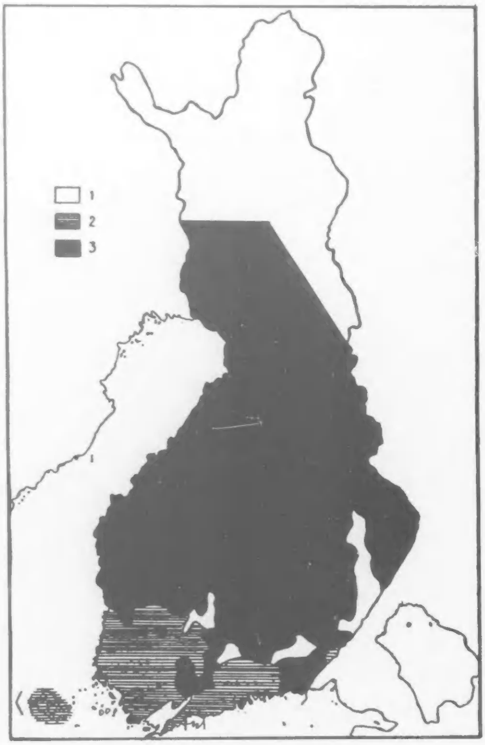

FIG. 2. Distribution of lakes of three trophic types (Järnefelt 1951). 1, oligotrophic; 2, eutrophic; 3, dystrophic.

time and the beginning of the growing season are delayed.

The growth rate has generally been higher in recent years for the three percid species, possibly because of eutrophication of the lakes and rivers (Fig. 8). Anttila (1967, 1970) pointed out that the eutrophication of Tuusulanjärvi resulted in an increased growth rate for the pikeperch, and the same has been noted in the brackish-water area off Helsinki (Seppänen 1970; Lehtonen 1972). Catch statistics and tagging experiments show an increase in the rate of exploitation, and this may partly explain the increased growth rate.

The areas of clear water may be said to be populated by fast-growing perch, as is seen from the following data (from Toivonen 1962; Toivonen et al. 1964; Sumari 1971):

	Lakes with slow-growing perch ($n=23$)	Lakes with fast-growing perch ($n=9$)	t	P
kg·ha^{-1}	12.5 ± 2.4	10.5 ± 3.0	0.52	<0.50
Pt mg·ℓ^{-1}	30.4 ± 4.3	18.3 ± 3.3	2.09	<0.05
µS·cm^{-1}	31.0 ± 4.8	15.0 ± 3.5	2.61	<0.01

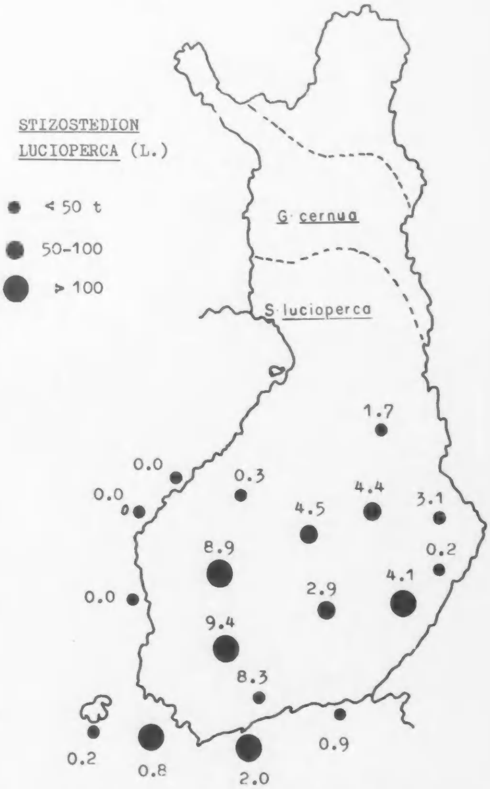

FIG. 3. Regional variations in catches of pikeperch in 1959. Data from Heikkinen (1960). The dashed lines indicate the northern distribution limits of ruff and pikeperch. The numerals by the dots indicate the catches of pikeperch as percentages of the total catch.

Population Dynamics

Size of populations and yield — Toivonen (1966) supplied some data on catch statistics and mortality rates for the pikeperch in Suokumaanjärvi. The population densities for perch have been studied in small lakes by poisoning (Toivonen 1962; Wikgren 1963; Toivonen et al. 1964; Sumari 1971), by seining (Wikgren 1964), and by tagging (Lind et al. 1969, 1970, 1971, 1972, 1974; Lind and Turunen 1971; Kukko et al. 1972a) and in rivers by electrofishing (Kännö 1968, 1969, 1971); and for ruff in small lakes by poisoning and in rivers by electrofishing. In addition, the perch population in the Gulf of Finland at Tvärminne has been estimated through diving (Sumari 1963). The average estimates of population densities were as follows:

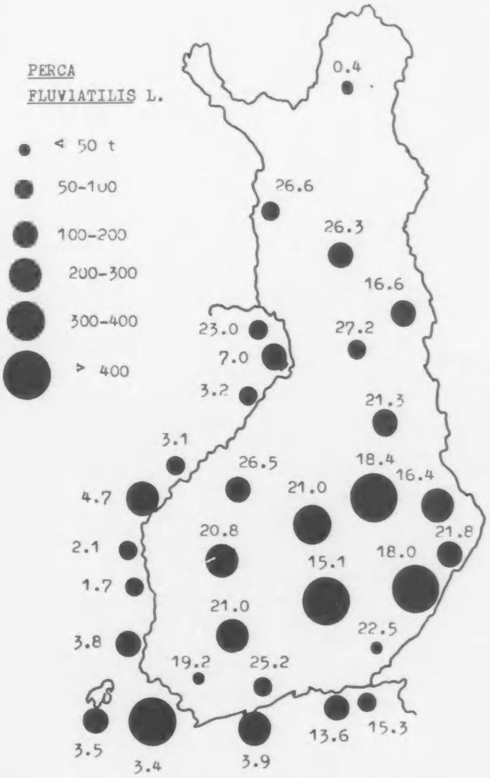

FIG. 4. Regional variations in catches of perch in 1959. Data from Heikkinen (1960). The numerals by the dots indicate the catches of perch as percentages of the total catch.

	kg·ha^{-1}
Pikeperch	
Tagging	6
Perch	
Poisoning	2–43
Seining	8
Tagging	4–90
Electrofishing	0–70
Ruff	
Poisoning	2–3
Electrofishing	0–19

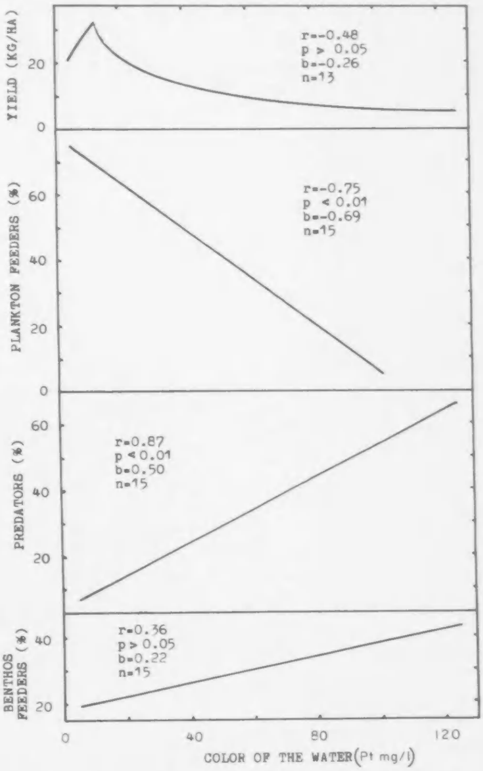

FIG. 5. Correlations between intensity of color of water in 15 large lakes and total yield and percentages of plankton feeders, predators, and benthos feeders in the yield. Data from Lagom (1962), Pulkkinen (1965), Shemeikka (1971), Mikkola (1972), Toivonen (1972), Seppovaara and Niemi (1973), Kaukoranta and Niemelä (1973), Huuskonen and Kostiainen (1973), Uusimäki (1973), Lind (1974), and Ollila (1974).

Only a few direct estimates of perch production have been made in Finland. Production was calculated on the basis of the population and growth rate, as in the work of Ricker (1946), Allen (1950), and Chapman (1968).

In Kourulampi, a small lake, the production of mature fish amounted to about 6.3 kg·ha^{-1}·yr^{-1}, or about 20% of the 31 kg·ha^{-1} standing crop (Lind et al. 1971). In Kiutajärvi the combined production of 0- and 1-yr-old perch amounted to 5.7 kg·ha^{-1}·yr^{-1}, or about 70% of the standing crop in these age-classes. The corresponding figures for mature perch were 4.4 kg·ha^{-1}·yr^{-1}, or about 41%; and those for the gonads, 1.2 kg·ha^{-1}·yr^{-1}, or 11%. The total production of the perch was estimated at 11.2 kg·ha^{-1}·yr^{-1}, or 60% of the standing crop (Lind et al. 1974).

Movements — The extent of movement of the pikeperch and the perch in large bodies of water do not differ very much (Fig. 9). The data also show that different parts of large bodies of water may be inhabited by isolated populations. The

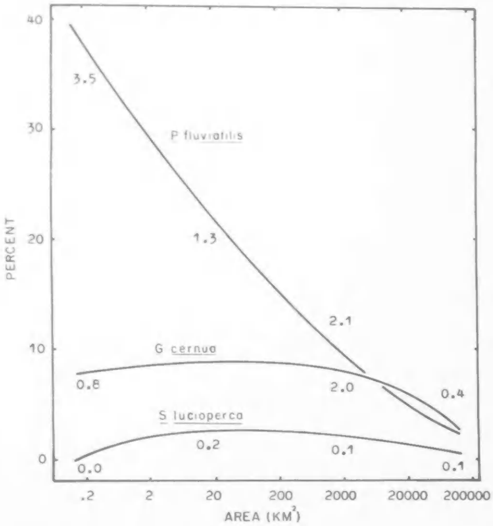

FIG. 6. Relationship (partly schematic) between size of water bodies and percentages of percids in the catches. Figures by the lines indicate yields in kilograms per hectare. Data from Lagom (1962), Pulkkinen (1965), Maataloushallituksen Kalataloudellinen Tutkimustoimisto (1970), Shemeikka (1971), Mikkola (1972), Huuskonen and Kostiainen (1973), Uusimäki (1973), Ollila (1974), and Finnish Game and Fisheries Research Institute, Fisheries Division (1974).

principal pattern of migration is seasonal; habitat requirements differ seasonally and percids migrate accordingly. For example, the perch spawning in the estuary of the Oulujoki River migrate out to sea to their growing and overwintering areas.

Year-class strength — Alm (1946, 1951) was the first to describe the year-class fluctuations in small-lake perch populations in detail, demonstrating that one strong age-class remains predominant for several years. This is true especially in the case of dystrophic lakes, in which a strong age-class may remain predominant for about 15 yr. In small eutrophic lakes the corresponding figure was <10 yr.

Later it was proposed (Kukko and Lind 1972) that this age-class structure is characteristic of perch populations in ponds, of which a number of individuals are found in nearly every part of the pond. These observations are supported by those (Lind 1976) made on *Coregonus albula*, which show a positive correlation between the duration of the age-class predominance and the intensity of color of the water.

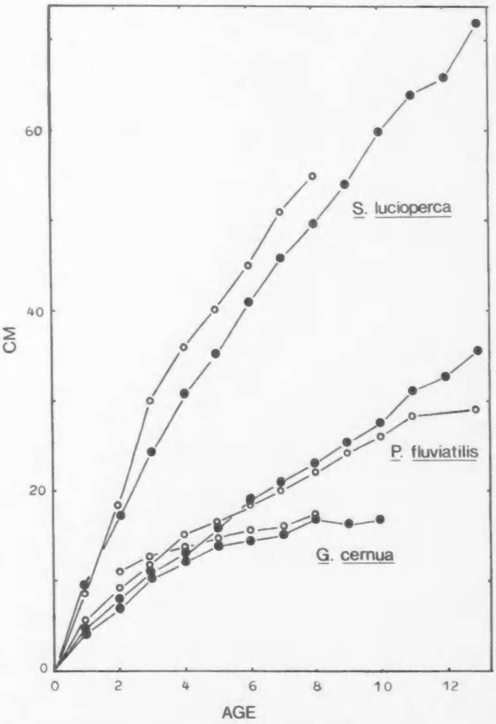

FIG. 7. Growth rates of perch, pikeperch, and ruff in freshwater (●) and brackish-water (○) areas during 1913–73. Data from Brofeldt (1915, 1917), Järnefelt (1917, 1921), Odenvall (1927), Jääskeläinen (1930), Segerstråle (1932, 1933), Järvi (1936, 1937, 1938, 1939), Halme and Hurme (1952), Lagom (1962), Seppänen (1970), Toivonen (1970), Karhumaa (1970), Lehtonen (1972), Lind et al. (1974), Hanski (1975).

Mortality rates — In Suokumaanjärvi the mortality rate of the pikeperch was 0.70, the natural mortality rate and the rate of exploitation being 0.20 and 0.50. The natural mortality rate decreased and the rate of exploitation increased with the age of the fish (Toivonen 1966). For the brackish-water areas around Åland, corresponding figures were 0.58, 0.39, and 0.19 (Toivonen 1969) and at Helsinki, 0.30, 0.25, and 0.05 (Lehtonen 1972).

In Lake Kiutajärvi the fishing mortality rate of age-group 1 perch was 0.07 (Lind et al. 1974). In the Gulf of Bothnia the mortality rate for perch was 0.58, the rate of natural mortality 0.48 and that of exploitation 0.10. The corresponding figures for perch tagged in the estuary of the Oulujoki River were 0.83, 0.66, and 0.17. The

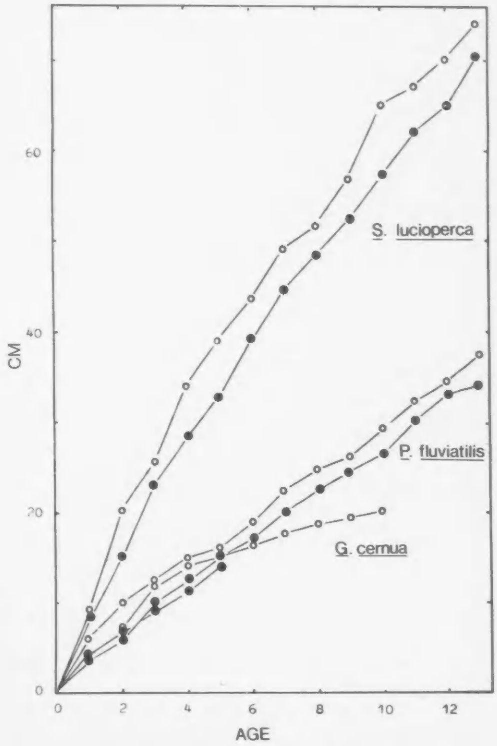

FIG. 8. Growth rates of the three percids during 1913–37 (●) and 1958–73 (○). (See Fig. 7 for data sources.)

average weights of fish in these two populations were 184 and 62 g, which explains the difference in the above mortality rates (Lind et al. 1975b).

Perch in various ponds showed increased survival with increasing darkness of the water and with decreasing trophic levels. A positive correlation between the maximum age of the fish and the intensity of color of the water was observed. Correlation coefficients were as follows (for sources of data see Fig. 7):

Ruff	$r = 0.87$	$P < 0.01$	$n = 8$
Perch	$r = 0.51$	$P < 0.05$	$n = 19$
Pikeperch	$r = 0.39$	$P > 0.05$	$n = 11$

In general, clear water results in fast growth and low age and humic water in slow growth and high age.

Survival of eggs and fry of perch — The number of eggs spawned was estimated on the basis of the standing crop, sex ratio, and number of eggs per female. The estimate for eggs spawned in some pond populations ranged from 2000 to 650,000 eggs·ha^{-1}. The survival rate of these eggs to the age of 1 yr ranged from 0.0001 to 1.1%. There was a negative correlation between density of mature fish and survival (Lind et al. 1969; Kukko et al. 1972b). In ponds treated with rotenone the number of mature perch was small when a new predominant age-group formed (Sumari 1971).

In Lake Kiutajärvi the estimated number of eggs spawned was about 700,000 eggs·ha^{-1}. The survival of these to the age of maturity was about 0.03% (Lind et al. 1974).

Environmental Toxins and Heavy Metals

Scattered information on concentrations of cadmium, lead, DDT and PCBs indicate low concentrations in the perch and pikeperch. High concentrations of mercury (Häsänen 1975; Lind and Hanski 1976) have been found in watersheds in agricultural areas and regions where cellulose industries are located, the Kymijoki, Kokemäenjoki, and Oulujoki rivers.

The perch and the pikeperch had high concentrations, while the ruff, only low levels. This difference may be explained on the basis of differences in food selection. In the sea off the town of Oulu during 1968–72 there was a positive correlation between both the length and weight of the perch and mercury concentration. There was no apparent correlation between distance from mercury source and the concentrations of mercury in the perch in the northeastern part of the Gulf of Bothnia, possibly because perch here migrate widely (Fig. 9). This conclusion is supported by observations made on the pike, which showed decreasing mercury concentrations with increasing distance from the mercury source, but pike did not move more than 16 km from their tagging place. In addition, these observations suggest that most of the mercury flowing into the sea sinks to the bottom not far from the source (Lind and Hanski 1976).

Häsänen (1975) noted a slight reduction in mercury concentrations in the sea off the Kymijoki River during the last few years, and corresponding observations have been made in Lake Päijänne (Paasivirta et al. 1975). An increase and decrease in mercury discharges to the sea off the town of Oulu led to corresponding fluctuations in concentrations of the metal in percids (Fig. 10). Maximum concentrations were found in perch and ruff about 5 yr after maximum discharges were observed. The time interval is approximately equal to the mean longevity of the species.

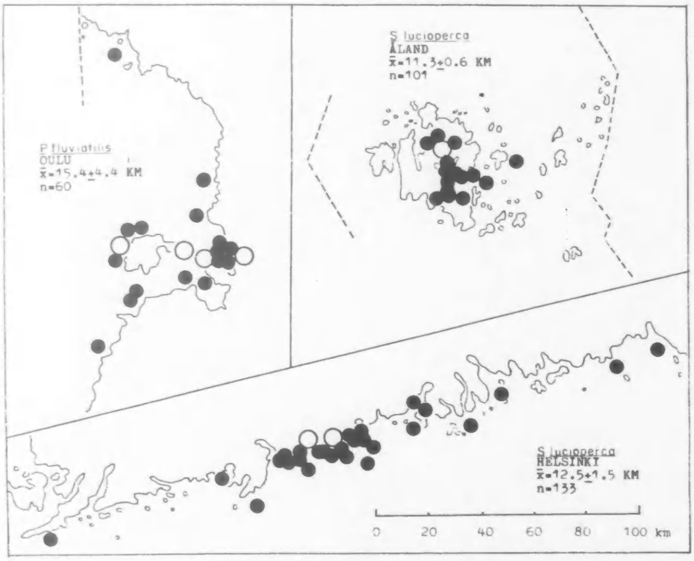
P fluviatilis
OULU
$\bar{x}$=15.4±4.4 KM
n=60
S lucioperca
ÅLAND
$\bar{x}$=11.3±0.6 KM
n=101
S lucioperca
HELSINKI
$\bar{x}$=12.5±1.5 KM
n=133
0
20
40
60
80
100 km

FIG. 9. Movements of pikeperch and perch in brackish-water areas. Dots are recapture locations of fish caught, tagged and released at sites indicated by circles. Data for the perch from Lind et al. (1975a), for the pikeperch tagged at Åland from Toivonen (1969), and those at Helsinki from Lehtonen (1972).

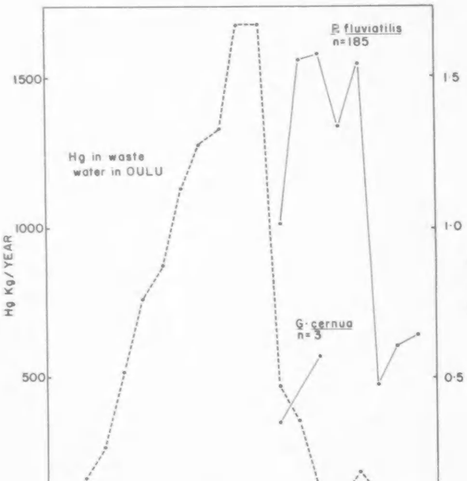

FIG. 10. Mercury concentrations in two percids from the sea off the town of Oulu during 1968–75, and mercury output from the cellulose factory of Oulu Osakeyhtio during 1957–75 (Lind and Hanski 1976).

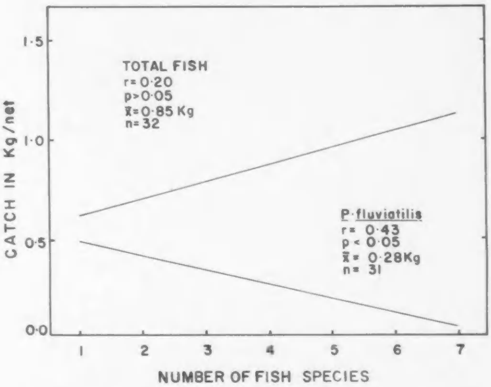

FIG. 11. Catches of perch and total fish obtained from series of gill nets in relation to the number of fish species; *n*, number of ponds and small lakes studied. Data from Maatalcushallituksen Kalataloudellinen Tutkimustoimisto (1970).

Position of Percids in the Community

Gymnocephalus cernua — This species is typically a prey fish. It is the smallest of the percids and is usually <20 cm long (Fig. 7). Carlin (1963) has shown that an increase in length of 1 cm improves the survival rate by 1–3%.

As a result of this, the mean age of the species is about 3–5 yr, and the mean maximum age about 7 yr. Its high rate of mortality is compensated for by its attainment of maturity at the age of 2 or 3 yr.

Perca fluviatilis — Perch are both prey and predators. Young perch feed on zooplankton, those of medium size mainly on benthic fauna, and large ones partly on benthic fauna and partly on fish. These food relationships exist also in ponds or small lakes populated only by perch. It is in these ponds or small lakes, however, that the species reaches its maximum population densities and production (Fig. 6).

The perch is not a very strong competitor. Population densities in ponds treated with rotenone decreased with an increase in the number of fish species (Sumari 1971). The same effect was noted in catches obtained from series of gill nets from several ponds and small lakes (Fig. 11). The catch of perch taken from a pond amounted to about 90 kg·ha^{-1} before stocking with brown and rainbow trout, and to about 1 kg·ha^{-1} after stocking (Lind et al. 1970, 1972). Two lots of brown trout were introduced into another pond in 1972–73, resulting in a decrease of the perch population. These studies indicated that the brown trout reduced perch populations. It is known that perch is one of the main sources of food for brown trout (e.g. Thorpe 1974).

In general, perch is intermediate between ruff and pikeperch in fish communities in Finland. The young perch is an object of prey, with a high mortality rate, whereas the older perch is partially predator, with a higher survival rate. The species is also intermediate with respect to its maximum age of 20 yr, mean maximum age of about 12 years, mean age of 5–6 yr, mean size of about 18 cm, and maturity at the age of 3–4 yr.

Stizostedion lucioperca — Pikeperch, with a low rate of natural mortality (Toivonen 1966, 1969, 1970), represents a major predator in fresh- and in brackish-water areas. The species reaches maturity at the age of 4–5 yr, attains a maximum age of more than 20 yr, a mean maximum age of about 15 yr, a mean age of 5–7 yr, and a mean size of more than 40 cm.

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Changes in Walleye (*Stizostedion vitreum vitreum*) Population in Rainy Lake and Factors in Abundance, 1924–75[1]

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CHEVALIER, J. R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924–75. J. Fish. Res. Board Can. 34: 1696–1702.

Annual commercial harvests of walleye (*Stizostedion vitreum vitreum*) from Rainy Lake steadily declined from 150,000 kg in the 1920s to 19,000 in the early 1970s; total (all species) harvests averaged 374,000 kg from 1924 to 1975, 45% greater than the MEI estimated allowable harvest. The walleye catch per unit of effort from commercial 102 mm gill nets declined from 43.63 kg/km in 1948 to 18.43 in 1969. Growth rate of walleye increased from 1959 to 1965, probably as a compensatory response to decreased abundance. The increased growth rate, in conjunction with heavy exploitation, caused the mean age of the walleye commercial catch to decline from 1957 to 1967. Both spring water levels and brood stock abundance were significant factors in walleye abundance 5 yr later. From multiple linear regression analysis, these two variables accounted for 65% of the variation in commercial walleye CUE.

Key words: Percidae, *Stizostedion*, walleye, population dynamics, abundance, yield, exploitation, water level, Rainy Lake, Ontario–Minnesota

CHEVALIER, J. R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924–75. J. Fish. Res. Board Can. 34: 1696–1702.

Les récoltes commerciales annuelles de doré jaune (*Stizostedion vitreum vitreum*) du lac à la Pluie diminuèrent régulièrement de 150 000 kg durant les années 1920 à 19 000 au début des années 1970; les récoltes totales (toutes les espèces) se chiffrèrent en moyenne à 374 000 kg de 1924 à 1975, 45% plus grandes que la récolte permissible estimée. Les prises de doré jaune par unité d'effort dans les filets maillants commerciaux de 102 mm diminuèrent de 43.63 kg/km en 1948 à 18.43 en 1969. Le rythme de croissance du doré jaune augmenta de 1959 à 1965, probablement une réponse compensatrice à une diminution d'abondance. Le rythme de croissance accru, couplé à une exploitation intense, entraîna une diminution de l'âge moyen des dorés dans les prises commerciales entre 1957 et 1967. Les niveaux d'eau au printemps et l'abondance du stock reproducteur sont tous deux des facteurs importants de l'abondance du doré jaune 5 ans plus tard. L'analyse de régression linéaire multiple indique que ces deux variables sont responsables de 65% de la variation dans les prises commerciales de doré jaune par unité d'effort.

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THE purpose of this paper is to describe the changes in the walleye, *Stizostedion vitreum vitreum* (Mitchell), population of Rainy Lake from 1924 to 1975 brought about by exploitation and spring water levels. Most of the population monitoring has been via the commercial fishery which used the same type of gear and sought the same species since the 1920s. Much of the information from pre-1967 presented in this paper was previously published by other investigators in a number of governmental reports.

Rainy Lake forms a portion of the Canadian–American International Boundary between Ontario and Minnesota at 48°42′N and 93°10′W. Development on the lake consists of two towns with a combined population of 20,000 people, about 2,000 private lakefront cottages and permanent homes, and about 38 summer tourist camps (maximum capacity of 1,500 guests). Domestic pollution has not been a problem. Commercial fishing has been a significant exploiter of the fish community since the late 1800s. The sport fishery, based almost completely on the walleye, has become of major importance during the last quarter century.

Thirty-six fish species, in 15 families, have been identified in Rainy Lake. The major sport species are walleye and northern pike (*Esox lucius*); of lesser importance are sauger (*Stizo-*

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TABLE 1. Physical and chemical (ppm except as indicated) characteristics of Rainy Lake.

Physical		Chemical	
Area (km²)		Total alkalinity	25
Lake	858.0	Total dissolved solids	57
Watershed	37,552	Conductivity (μmhos)	44
Depth (m)		pH	6.8–7.8
Mean	9.94	Dissolved oxygen	3
Maximum	49.07	(late summer hypolimnion)	
Volume (10^9 m³)	8.53	Morphoedaphic index (metric)	5.74
Flushing rate (days)	359	Sulphate ion	8.0
Shoreline (km)		Total phosphorus	0.027
Basin	1,495	Chlorides	5.65
Island	1,068	Nitrogen	
Shoreline Dev. Factor	14.4	Ammonia	0.03
Littoral zone (% ≤ 6.1 m)	42	Nitrite	0.006
Transparency (m)	2.04	Nitrate	0.002
		Total Kjeldahl	0.40

stedion canadense), yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieui*), muskellunge (*Esox masquinongy*), and black crappie (*Pomoxis nigromaculatus*). The major commercial species are walleye, northern pike, lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*), burbot (*Lota lota*), and white sucker (*Catostomus commersoni*); of lesser importance are lake sturgeon (*Acipenser fulvescens*), rock bass (*Ambloplites rupestris*), yellow perch, sauger, and black crappie. Both black crappie (unknown date) and smallmouth bass (1921) were stocked in the lake and probably introduced.

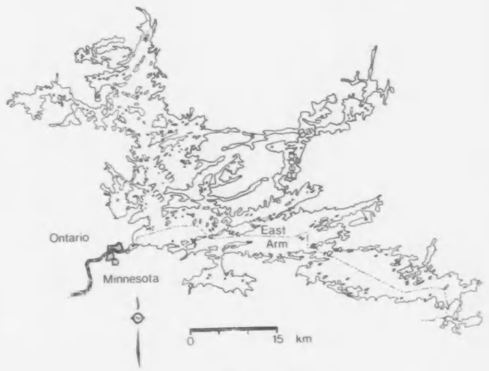

FIG. 1. Rainy Lake.

Physical and Chemical Characteristics

Coniferous forest covers most of the Rainy Lake watershed, 16% of which is water. The lake basin is irregular with 1495 km of shoreline which is complemented by another 1068 km of shoreline associated with some 1600 islands (Table 1). The 858 km² lake is composed of three geographically distinct sections (Fig. 1): North Arm, East Arm, Redgut Bay. Seventy percent of the watershed and 75% of the lake area are within Ontario jurisdiction.

Precambrian rock underlies most of the lake basin. Exposed on islands and shore are Keewatin volcanic rocks, Couchiching sedimentary rocks, Windigokan sediments, Algoma granite, Animikie sediments, and Keeweenawan diabase. The Pleistocene glaciers left deposits of calcareous and noncalcareous till, bluish grey calcareous clays and associated fluvioglacial sands and gravels (Pye 1968). The eastern boundary of postglacial Lake Agassiz may have touched Rainy Lake's southwestern shore because here the Laurentian Shield ends and the lowlands characteristic of Lake Agassiz begin.

Probably owing to its Precambrian origin, the lake is chemically unproductive as evidenced by the low values for total alkalinity (25 ppm), total dissolved solids (57 ppm), and total phosphorus (0.027 ppm). The morphoedaphic index (Ryder 1965; Ryder et al. 1974; in metric units) of 5.74 categorizes Rainy as mesotrophic.

A hydroelectric dam was constructed on the outlet, Rainy River, in 1909 and controls the lake levels under general regulations established by the International Joint Commission. A gradual fall and winter drawdown for power generation and a spring and summer build-up have been normal. In 1969, revisions to the operating regulations by the I.J.C. allowed for a zone of acceptable lake levels on specific dates. At present, these regulations dictate a minimum lake level of 336.93 m and a maximum of 337.36 m during the first 2 wk of May, which usually encompasses the walleye spawning season. However, only the upper levels of this range are considered satisfactory for properly inundating walleye spawning areas.

History of the Fishery

Commercial fishing — The first recorded commercial fishery on Rainy Lake (1885) was a pound-net lake sturgeon fishery; the sturgeon were utilized for roe, the flesh being discarded. An extensive trapnet fishery developed for ciscoes at the turn of the century and continued until the 1920s. In 1904, the first gillnet fishery began (lake whitefish) but pound nets remained more popular than either gill nets or trap nets until the 1920s. Since the 1920s, gill nets have been the primary gear and walleye, northern pike, and lake whitefish the primary target species.

Annual harvest totals were first reliably recorded in 1924. From 1924 to 1975, the commercial fishery (Ontario and Minnesota) averaged a total annual harvest of 374,308 kg (Fig. 2). This level of harvest exceeded the morphoedaphic index predicted allowable harvest of 258,682 kg by 45%. Although the total commercial harvest was somewhat erratic, an overall decline during this time span is evident. Annual walleye commercial harvest declined steadily from 150,000 kg in the mid-1920s to 19,000 kg in the early 1970s and the percentage contribution to the commercial catch declined from 30% to less than 10%. Because of the good economic return from walleye, trends in harvest were probably indicative of trends in abundance.

The present commercial fishery is managed by regulations on amount of gear, mesh size, areas fished, and size of allowable fish. Ontario, which accounts for more than 80% of the annual harvest, raised minimum gillnet mesh size in 1970 from 102 to 108 mm to reduce the harvest of immature walleye and began to establish walleye quotas for some area-specific fisheries and terminate others through attrition. In 1972, Ontario closed its commercial fisheries in the East Arm and Redgut Bay because of mercury levels above federal standards in walleye and northern pike. In 1974, these fisheries were reopened when "blending" processes reduced levels of mercury in fish products below the acceptable level.

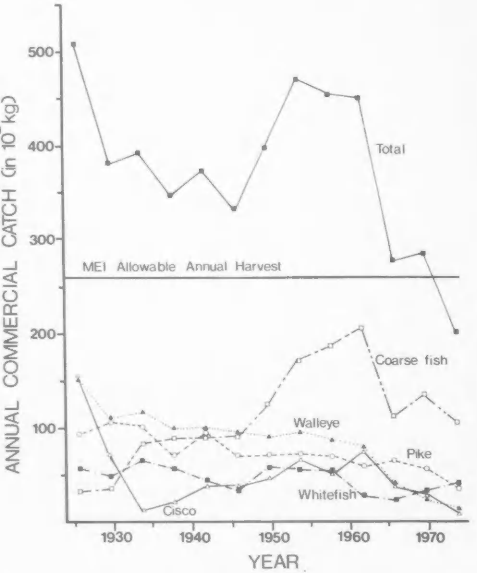

FIG. 2. Commercial fishing harvests from Rainy Lake by 4-yr annual means, 1924–1975.

Minnesota ended its lake sturgeon fishery before 1938. During this same era, commercial fishing in the western end of the East Arm was terminated, primarily to protect the major walleye spawning population in the Black Bay area. Minnesota is now transferring commercial fishing effort from walleye to lake whitefish by attritionally changing licencee's minimum mesh size from 102 to 133 mm.

Sport fishery — The sport fishery is based almost completely on walleye and northern pike. Although no complete creel surveys have been conducted because of the large size and great irregularity of the lake, the 38 summer tourist camps, 2,000 cottages and homes, and the two towns with 20,000 residents probably exert a considerable influence on the fish populations. Returns of 1,191 walleye within the first year after 7,315 were tagged during 1957–74 suggested that the sport and commercial walleye harvests were about equal: 48% of the returns were from the sport fishery (Bonde et al. 1965; Caldwell unpublished data). The tagging information further suggests that some relatively discrete segments of the population are exploited principally by the sport fishery and others by the commercial fishery.

Changes in the Walleye Population

Catch per unit effort — Catch in weight of walleye and effort by length of 102 mm mesh gill nets per day were recorded from 1948 through 1969 (minimum legal mesh sizes were increased in 1970) and used as an index of abundance (Ricker 1975). Catch per unit of effort, calculated from the regression equation (Fig. 3; $P < 0.01$), declined from 43.63 $\text{kg} \cdot \text{km}^{-1} \cdot \text{day}^{-1}$ in 1948 to 18.43 in 1969, a drop of 58%.

Growth — Mean total lengths of age IV walleye (back-calculated from IV+ to IV) sampled from the North Arm commercial catch in August and September were regressed on the years of catch for 1959–65 (Fig. 4). The significant regression ($P < 0.01$) indicated that mean total lengths of age IV walleye had increased from 37.34 cm in 1959 to 41.60 cm in 1965. The high correlation coefficient ($r = 0.98$) associated with these data suggested that the observed increases in mean total lengths were the result of progressive increases in growth rate. Although samples of total length from the East Arm commercial walleye catch were insufficient for regression analysis, they did suggest a similar increased growth rate even though East Arm age IV walleye were smaller (approximately 20%)

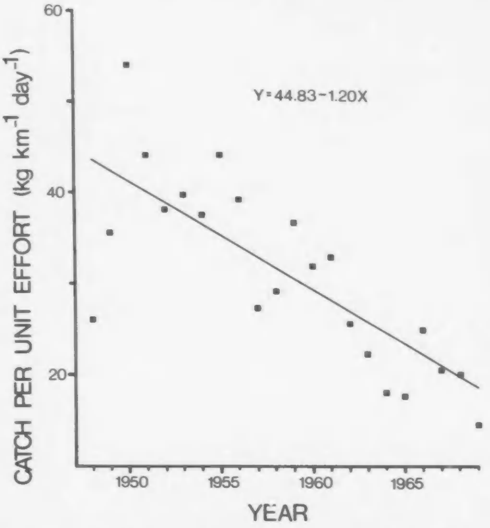

FIG. 3. Walleye catches per unit of effort (kg·km^{-1}·day^{-1}) from commercial 102 mm gill nets on Rainy Lake, 1948–69.

than their North Arm cohorts (Johnson et al. 1966). The increased growth of Rainy Lake walleye was probably a compensatory response to decreased abundance, as found in various other fish populations (Healey 1975; Kipling and Frost 1970; Parsons 1967; Regier and Loftus 1972).

Growth of walleye in the North Arm was faster than in northwestern Minnesota's Red Lakes (Smith and Pycha 1961) and Many Point Lake (Olson 1957), similar to that in Minnesota's Lake of the Woods (Heyerdahl and Smith 1972) and Manitoba's West Blue Lake (Kelso and Ward 1972) and slower than in Lake Erie (Deason 1933) and Lake Huron's Saginaw Bay (Hile 1954).

Age structure — Mean ages of walleye from the commercial catch, calculated from the regression equations (Fig. 5, $P < 0.05$), decreased in the North Arm from 5.33 in 1957 to 3.63 in 1967; in the East Arm, from 6.53 in 1955 to 4.37 in 1967. The rates of decline were similar in the two areas as evidenced by the similar slopes of the regression equations, but changes in the East Arm ages apparently lag behind the North Arm by approximately 5 yr.

Before 1964, age III walleye contributed little to the commercial catch in the North Arm. However, in 1964, 1965, and 1967, age III walleye constituted 43, 63, and 35% of the catch, respectively (Caldwell 1964; Johnson et al. 1966; Caldwell unpublished data). In the East Arm during the 1950s, more than 50% of the walleye commercial catch was contributed by age VII or older fish; by the mid-1960s, less than 10% (Bonde et al. 1965; Johnson et al. 1966; Caldwell unpublished data).

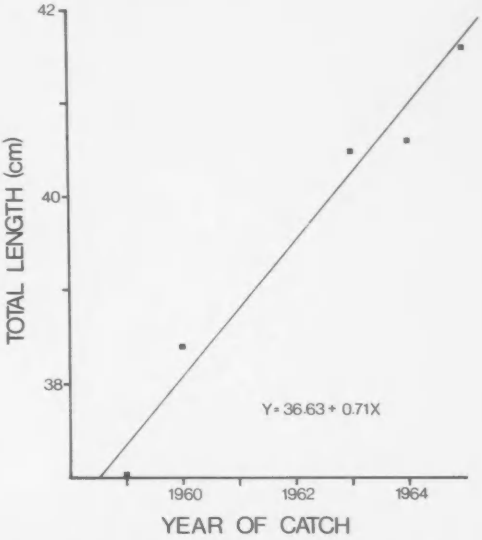

FIG. 4. Mean total lengths of age IV walleye (back-calculated from IV+ to IV, 35 fish per sample except 13 in 1959) from the commercial 102 mm mesh gill net catch, North Arm, 1959–1965.

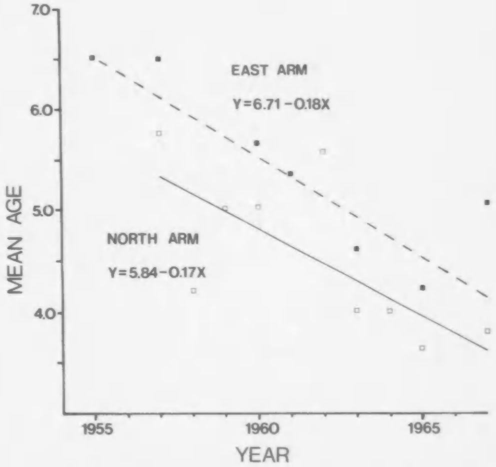

FIG. 5. Mean ages of walleye from the commercial 102 mm mesh gill net catches in late August and early September for the North Arm (1957–67) and the East Arm (1955–67); sample sizes ranged from 66 to 192.

The observed decreases in mean age of walleye in the commercial catch were probably to a large degree the result of the increased growth of walleye. As the fish grew faster, they became increasingly vulnerable to the 102 mm gill net at an earlier age, thus decreasing the mean age of the catch. Hamley and Regier's (1973) studies on gillnet selectivities of walleye demonstrate that this certainly may have occurred at the ages and sizes of walleye observed in Rainy Lake. Since walleye CUE from commercial 102 mm gill nets did not increase over this time period, the increased contribution of younger age-groups has probably been at the expense of older age-groups — essentially, the catch curve (age vs. relative frequency of the catch) shifted leftward towards a younger catch. Since walleye are increasingly vulnerable to this gear up to approximately 65 cm (Hamley and Regier 1973), or age X walleye from Rainy Lake, the loss of older age-groups from the commercial catch probably reflects a similar loss from the walleye population.

Factors Influencing Walleye Abundance

Spring water levels — Spring water levels on Rainy Lake were investigated as being an important factor in walleye spawning success because of similar declines in abundance in all sections of the lake. Lake shoal spawning seems to be common in Rainy Lake, as has been found in other walleye populations (Eschmeyer 1950; Everman and Latimer 1910; Johnson 1961; Kingsbury 1948; Rawson 1957). Of 68 random sections of North Arm shoreline examined in the spring of 1964, 14 contained walleye eggs (Caldwell 1964); of 30 suspected spawning shoals in the East Arm examined in the spring of 1965, 16 had been utilized (Johnson et al. 1966). In both studies, eggs were most abundant on beaches with gravel, rubble, or shingle rock in waters less than 0.3 m deep. Johnson et al. (1966) stated that the extent to which the clean gravel beaches, established by wave action at normal summer levels, are flooded in the spring determines whether spawning occurs on satisfactory areas or whether the fish are forced to spawn on less favorable bottom types where the chance of egg survival is poor. Johnson (1961) clearly demonstrated the importance of spawning substrate on walleye egg survival in several Minnesota lakes.

The annual walleye commercial CUEs from 102 mm mesh gill nets for 1948–69 were compared with the spring water levels 4, 5, and 6 yr earlier. Spring water levels were determined as the mean elevations at the dam 1–15 days after "ice-out." CUE was calculated as the weighted average of CUEs from each of the three major sections of the lake. All reliable catch data were used irrespective of season or location of catch. The 4, 5, and 6-yr differentials were chosen because age-groups IV–VI constituted the bulk of the commercial catches over the sampling period. The correlation coefficients of 0.48, 0.71, and 0.47 for 4, 5, and 6-yr differentials respectively, were all significant ($P < 0.05$) but the 5-yr differential seemed to be more highly related to water levels. The regression equation of CUEs on spring water levels 5 yr earlier was $Y = -93.26 + 16.81X$, and the coefficient of determination (R^2) indicated that spring water levels accounted for 50% of the variation in the commercial CUE (Fig. 6).

Brood stock — Because of the apparent precipitous decline in walleye abundance and the inherent possibility of reduced and inadequate reproductive capacity, the relation of brood stock abundance to future population abundance was also investigated. The best continuous index to walleye abundance on Rainy Lake has been the commercial CUE. Analysis of the relationship between CUE (progeny abundance) and CUE from 5 yr earlier (brood stock abundance) showed progeny abundance to be significantly related ($P < 0.01$) to brood stock following the equation $Y = 6.51 + 0.64X$ (Fig. 6). (The 5-yr differential was again used since the average age of all the commercial catch during this time period was about 5 yr.) The coefficient of determination (R^2) indicated that brood stock abundance accounted for 44% of the variation in walleye abundance 5 yr later.

The combined influence of water levels and brood stock was measured by multiple linear regression. The resulting equation was $Z =$

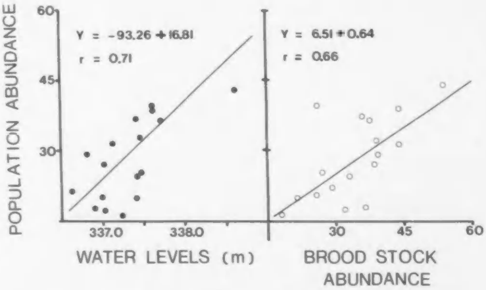

FIG. 6. Indexes of walleye population abundance in relation to spring water levels and indexes of brood stock abundance 5 yr before. Abundance indexes are commercial 102 mm mesh gillnet catches per unit of effort ($kg \cdot km^{-1} \cdot day^{-1}$).

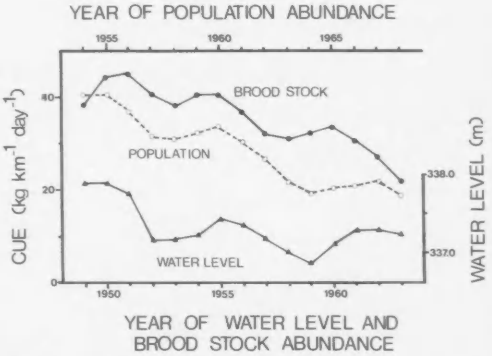

FIG. 7. Trend of walleye population abundance in Rainy Lake, 1954–68, in relation to spring water levels and brood stock abundance 5 yr before (3 yr running averages). Abundance indexes were commercial 102 mm mesh gill net catches per unit of effort (CUE). Modified and updated from Johnson 1967.

$-58.39 + 0.42X + 9.9Y$ where $X =$ spring water levels, $Y =$ brood stock abundance, and $Z =$ progeny abundance 5 yr later. Analysis of variance indicated that both regression coefficients were different from zero ($P < 0.01$) and that the addition of either significantly ($P < 0.05$) improved the descriptive model. Spring water levels and brood stock abundance together accounted for 65% of the variation in the commercial walleye CUE. Although water levels have fluctuated more than the two CUE variables (Fig. 7), the sinuosities of the curves were similar. The 3-yr running averages in Fig. 7 were used for graphical illustration only and not for statistical analyses.

Discussion

Spring water levels in Rainy Lake undoubtedly effect walleye year-class strength through spawning success on lake shoals. Busch et al. (1975) showed that spawning success on lake shoals was important in determining year-class strength of Lake Erie walleye. Other investigators have indicated the importance of spring water levels and flows on walleye spawning success (Derksen 1967; Olson and Scidmore 1962; Priegel 1970). Svardson and Molin (1973) suggested that pikeperch (*Stizostedion lucioperca*) year-classes are effected by spring water levels in Sweden. Although spawning habits of pikeperch and walleye differ considerably, lower water levels apparently cause both species to spawn in less than optimum locations or conditions.

Brood stock abundance probably regulates future population size through the number of eggs laid and the subsequent recruitment to the population. Because of the inherent reproductive capacity of walleye, this condition has seldom been documented. Christie (1968) implicated this factor as a partial explanation for the decline of some fish populations in the Great Lakes. Eshenroder (1977) suggested a positive relationship between brood stock abundance and recruitment may exist in the Saginaw Bay yellow perch population.

Exploitation of the walleye population in Rainy Lake acts to depress the number of spawners. This depressing effect may have intensified in the recent past because of the observed greater exploitation of younger age-groups and the subsequent loss of older age-groups. To meet the conditions of Abrosov's (1969) model for maintaining a stable fishery for European percids, average age of the Rainy Lake walleye catch should be 5.5–6.0 yr. However, average age of the catch during the mid-1960s was less than 4.5 yr in both the North and East Arms.

There is an additional grave implication for the walleye population because of the younger age structure. With fewer important age-groups in the population, more dependence is placed on individual year-classes. Increased dependence on individual year-classes lessens population resilience to physical and biological stresses and so may cause greater population fluctuations and instability.

From the information presented in this paper, it is not possible to conclude which of the two variables, spring water levels or brood stock abundance, has played the major causative role in the decline of the Rainy Lake walleye population. One can reason that water levels are of major importance because of their effect on population abundance as well as a partial effect on brood stock abundance. However, one may also hypothesize that exploitation decreased the population to the point where brood stock and recruitment were correlated and then the influence of spring water levels became more pronounced because of the need to maximize recruitment.

Future management strategy for increasing the Rainy Lake walleye population might take into account an optimization of spring water levels. The minimum lake levels established by regulation in 1969 are not sufficient for improving walleye spawning conditions, as evidenced by Fig. 7. Since the exact role of exploitation on the population is unclear, management might opt for the experimental approach by maintaining the present exploitation rate (both sport and commercial must be considered). Then, if the optimized spring water levels do not increase the population to the desirable level, one will have a better understanding of the role played by exploitation and can regulate accordingly.

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Factors in the Declining Contributions of Walleye (*Stizostedion vitreum vitreum*) to the Fishery of Lake Nipissing, Ontario, 1960–76[1,2]

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ANTHONY, D. D., AND C. R. JORGENSEN. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960–76. J. Fish. Res. Board Can. 34: 1703–1709.

Analysis of the 1960–76 creel survey data for Lake Nipissing and relevant data collected by the Lake Nipissing Fisheries Assessment Unit from 1969 to 1976 showed a generally declining walleye (*Stizostedion vitreum vitreum*) contribution to the Lake Nipissing fishery. Variable year-class strengths alone did not adequately account for the changes. Overexploitation of the resource was strongly suggested by decreased catches per unit of effort, recruitment of younger walleye (many of which probably never spawned) into the fishery at least after 1968, and increased growth rate. The population is probably affected as well by climatic factors, interactions with white suckers (*Catostomus commersoni*), northern pike (*Esox lucius*), and yellow perch (*Perca flavescens*), and by technology and watershed influences.

Key words: walleye, Lake Nipissing Ontario, Lake Nipissing fishery, Percidae, *Stizostedion*

ANTHONY, D. D., AND C. R. JORGENSEN. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960–76. J. Fish. Res. Board Can. 34: 1703–1709.

L'analyse des données recueillies lors de recensements au panier entre 1960 et 1976 au lac Nipissing et des données pertinentes recueillies par l'Unité d'évaluation des pêches du lac Nipissing entre 1969 et 1976 révèle qu'en général la contribution du doré jaune (*Stizostedion vitreum vitreum*) à la pêcherie du lac Nipissing est allée en diminuant. Les variations d'abondance des classes d'âge ne suffisent pas, à elles seules, à expliquer les changements. La diminution des prises par unité d'effort, le recrutement de jeunes dorés jaunes (dont plusieurs n'ont probablement jamais frayé) dans la pêcherie, du moins après 1968, et le rythme de croissance accéléré suggèrent fortement la surexploitation de la ressource. La population est probablement affectée aussi par des facteurs climatiques, des interactions avec le meunier noir (*Catostomus commersoni*), le grand brochet (*Esox lucius*) et la perchaude (*Perca flavescens*), et par les effets de la technologie et du bassin hydrographique.

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THIS paper discusses the generally declining trend in walleye (*Stizostedion vitreum vitreum*) contribution to the sport fishery of Lake Nipissing between 1960 and 1976. The lake (Fig. 1) is in northeastern Ontario at 46°17′ N and 80°00′ W. With a surface area of 855 km², it is the fourth largest lake entirely within the boundaries of the Province, and is primarily a sportfishing lake, walleye and yellow perch (*Perca flavescens*) being the principal sport species among the 41 species comprising the ichthyofauna.

Official records which go back to 1885 show that until the turn of the century the fishery (sport and commercial) was based almost exclusively on walleye, and that between 1885 and 1921 over 229,000 kg were harvested from the lake, mainly by the commercial fishery (54,000 kg between 1885 and 1889, and 174,700 kg between 1918 and 1921). Although this species, thought

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[1] This paper forms part of the Proceedings of the Percis International Symposium (PERCIS) convened at Quetico Center, Ontario, September 24–October 5, 1976.

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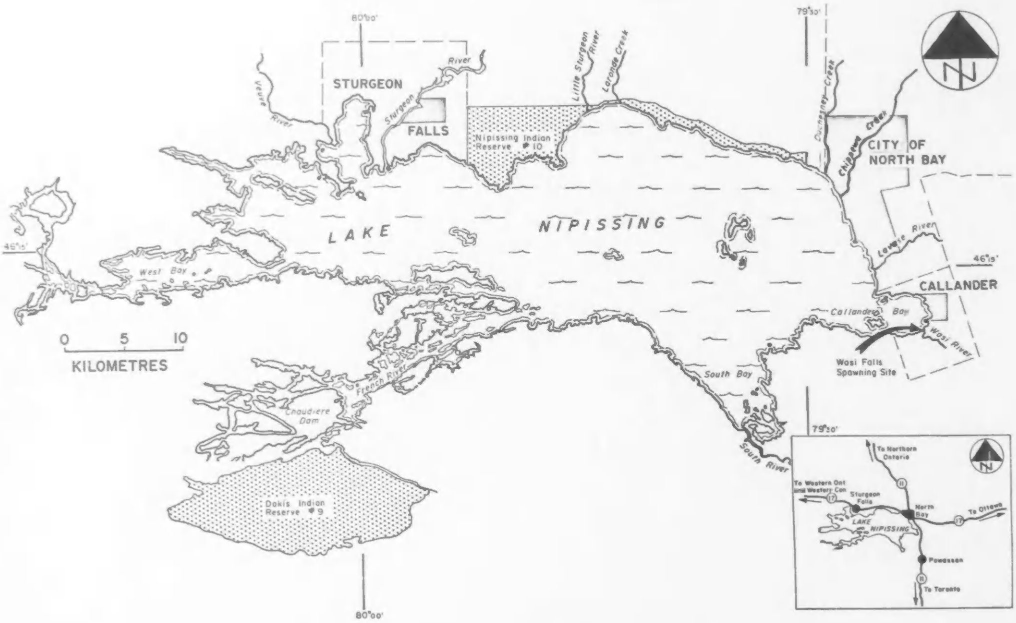
80°00'
79°30'
STURGEON
FALLS
Veuve River
Sturgeon River
Little Sturgeon River
Lavigne Creek
Nipissing Indian Reserve # 10
Duchesnay Creek
Chippewa Creek
CITY OF NORTH BAY
LAKE
NIPISSING
West Bay
46°15'
La Vase River
CALLANDER
Callander Bay
Wasi River
Wasi Falls Spawning Site
South Bay
South River
French River
Chaudiere Dam
Dokis Indian Reserve # 9
0 5 10
KILOMETRES
N
To Northern Ontario
To Western Ont and Western Can
11
17
Sturgeon Falls
North Bay
To Ottawa
LAKE NIPISSING
Powassan
To Toronto

FIG. 1. Location map of Lake Nipissing, Ont.

by some biologists to be of the "blue variety," i.e. the blue pike (*Stizostedion vitreum glaucum*), was abundant, the intensive fishery is considered to have severely depleted the stock by the early 1920s. As a result, walleye was removed from the commercial fishery in 1922; and between 1920 and 1934 nearly 13 million walleye fry were planted in the lake (10.8 million between 1920 and 1930, and 2 million in 1934). It was thought at that time that the combination of intensive fishing and extensive stocking would result in replacement of the "inferior blue variety" by the "superior yellow variety" (walleye).

Whether the subsequent success of the walleye population, and the consequent reputation of the lake for its walleye fishery, can be attributed to this scheme cannot be verified. Blue pike, nevertheless, does not now occur in the lake, if indeed it did previously occur therein. However, some morphometric characteristics of the present walleye population suggest possible introgression with the blue pike, a possibility which awaits detailed investigation.

Fluctuating but generally declining walleye contributions to the harvest during the last decade, declining catch per unit of effort (CUE), the age composition of the catch, and similar factors suggested possible overexploitation, perhaps indicating need for applying more effectual management practices to the entire fishery resource of the lake. Management, from the 1930s until 1969, was restricted to creel surveys and regulation enforcement directed almost exclusively at walleye, little attempt being made at managing the fish community as a whole.

Materials and Methods

The data utilized in this study are primarily those collected by the Lake Nipissing Fisheries Assessment Unit from 1969 to 1976 and the official creel survey figures dating back to 1960. The data are, however, incomplete; some inferences derived from them may therefore have to be modified as on-going research contributes more information.

Since much of the creel survey data, especially those for the pre-1967 period, lack various essential details, the main data used are those for 1967–76, particularly those for 1972–76. Conclusions concerning winter and summer harvests are based on the 1972, 1973, and 1976 harvest data since the data for these years are complete and, as far as could be determined by extrapolation, conclusions drawn from them were broadly applicable to the harvests of other years. The age composition of the walleye fishery and the growth rate of the species in the late 1960s and 1970s are based on random samples from the creels of 1967–68 and 1972–75.[3]

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[3] No creel survey was conducted in 1967, but a random sample was taken from angler catches during May and June.

TABLE 1. Species compositions (%) of the creel surveys, Lake Nipissing, Ont., 1960–76. Values for winter and summer respectively, shown in parentheses. Surveys not conducted in 1967 and 1971.

			% composition of year's total			
Year	Total	No. of fish counted	Walleye	Perch	Pike	Others
1960	5,499	(— , 5,499)	76 (—, 76)	0	21 (—, 21)	3 (—, 3)
1961	3,707	(67, 3,640)	67 (22, 68)	8 (0, 8)	24 (61, 23)	1 (16, 1)
1962	4,833	(2,903, 1,930)	42 (33, 55)	5 (2, 9)	46 (57, 30)	7 (7, 6)
1963	11,858	(3,300, 8,558)	63 (29, 76)	8 (4, 10)	24 (50, 14)	5 (17, 0)
1964	5,953	(1,231, 4,722)	52 (18, 61)	9 (12, 8)	37 (60, 31)	2 (10, 0)
1965	8,845	(1,828. 7,017)	48 (27, 53)	10 (18, 8)	30 (50, 25)	12 (5, 14)
1966	7,522	(1,807, 5,715)	46 (24, 53)	15 (19, 14)	32 (49, 27)	7 (8, 6)
1968	5,560	(4,048, 1,512)	37 (27, 62)	38 (46, 18)	22 (24, 17)	3 (3, 3)
1969	8,276	(6,001, 2,275)	40 (41, 39)	39 (39, 40)	16 (16, 15)	5 (4, 6)
1970	13,851	(— , 13,851)	47 (—, 47)	34 (—, 34)	14 (—, 14)	5 (—, 5)
1972	14,545	(5,358, 9,187)	30 (27, 32)	38 (35, 40)	24 (24, 24)	8 (14, 4)
1973	31,521	(19,138, 12,383)	20 (18, 24)	49 (47, 51)	25 (28, 20)	6 (7, 5)
1974	9,639	(— , 9,638)	50 (—, 50)	33 (—, 33)	15 (—, 15)	1 (—, 2)
1975	4,674	(— , 4,674)	44 (—, 44)	35 (—, 35)	15 (—, 15)	6 (—, 6)
1976	9,125	(6,198, 2,927)	32 (27, 44)	37 (39, 33)	16 (16, 16)	15 (18, 7)

Walleye Contributions to the Fishery

The species compositions of the creel for 1960–76 (Table 1) show the fluctuating contributions of walleye to the fishery and the declining predominance of the species. In most years, walleye contributed a much lower percentage of the winter than of the summer catch, while the percentage of perch in the winter harvest showed a generally increasing trend over the years, exceeding the percentage of walleye in the catch for 4 of the 5 years between 1968 and 1975 for which data are available; and during the same period (1968–75), when the percentage of walleye in the summer catch was declining, the percentage of perch rose substantially.

Though the annual fluctuations in the walleye contribution indicated in the creel may reflect to various extents variable year-class strengths (Parsons 1970), and/or the amount of fishing effort, angler skill, and the efficiency of the survey (Martin and Fry 1972), the generally marked downward trend suggests possible overexploitation and declining abundance of the resource.

The declining predominance of walleye is further exemplified in the estimated number of this species in the harvests of 1972, 1973, and 1976 compared with the number of perch (Table 2): walleye constituted 24.2% of the estimated number of fish taken in the winter harvest compared with 35.5% for perch; 31.3% of the number in the summer catch compared with 40.4% for perch; and 30.0% compared with 39.5% of the total harvests of these years. However, in estimated total weights harvested (Table 2), the contributions of walleye far exceeded those of perch.

Age and Size Compositions of the Catches

The age distributions of the 1967–68 and the 1972–75 samples (Table 3) suggest that the percentage of older fish in the fishery has declined since 1967–68, and that younger fish were entering the fishery. Comparison of the mean distribution of the 1967–68 sample with that of the 1972–75 sample shows that the percentages of fish aged 5 yr and older in the catch decreased markedly during the latter period while the percentages of 3- and 4-yr-olds increased. Fish more than 5 yr old comprised 33% of the 1967–68 sample compared with 18% of the 1972–75 sample; and specimens less than 5 yr old constituted 35% of the 1967–68 sample but 60% of the 1972–75 sample.

In 1967–68, the most heavily exploited age-groups were the 4–6-yr-olds, especially the 5-yr-olds, but during 1972–75 the most heavily exploited were the 3–5-yr-olds, especially the 4-yr-olds. Likewise, whereas in 1967 and 1968 3-yr-old specimens made up approximately 9 and 2%, respectively of the samples, in each of the 4 years from 1972 to 1975 this age-class comprised much higher percentages of the samples (approximately 24, 20, 28, and 15%, respectively).

Though these differences may be partly due to differences in sample size, they, nevertheless, strongly suggest a heavily fished population, especially when considered in conjunction with the

TABLE 2. Percentages of walleye and other species in the estimated numbers and weight (kg) of fish taken in the sport fishery of Lake Nipissing, winter and summer 1972, 1973, and 1976.[a]

	Total		Number				Weight			
Year	Number	Biomass to weight	Walleye	Perch	Pike	Others	Walleye	Perch	Pike	Others
					Winter					
1972	70,240	42,510	28.1	27.7	26.0	18.2	25.3	10.4	50.6	13.7
1973	78,780	50,898	19.7	37.9	35.8	6.6	16.7	13.3	65.4	4.6
1976	129,155	68,123	24.9	38.3	19.0	17.8	25.7	16.5	42.5	15.3
Total	278,175	161,531	24.2	35.5	25.5	14.8	22.8	13.9	51.8	11.5
					Summer					
1972	428,100	246,775	32.9	36.0	24.0	7.1	31.1	14.2	49.1	5.6
1973	425,640	215,064	24.0	51.0	20.0	5.0	25.9	22.9	46.7	4.5
1976	387,575	363,974	37.4	33.6	25.5	3.5	58.1	8.1	32.1	1.7
Total	1,241,315	825,813	31.3	40.4	23.1	5.2	41.7	13.8	41.0	3.5
Total Summer–Winter	1,519,490	987,344	30.0	39.5	23.5	7.0	38.6	13.8	42.8	4.8

[a] These years were selected because the census data are complete and, as far as could be determined, conclusions drawn from them are broadly applicable to other years.

TABLE 3. Percentages of walleye of various ages in random samples from Lake Nipissing creel surveys for 1967, 1968, and 1972–75.[a]

		Age (years)										
Year	No. of fish sampled	1	2	3	4	5	6	7	8	9	10	Mean age (years)
1967	99		1.0	9.1	24.3	*26.3*	21.1	10.1	6.0	2.0		5.3
1968	166			2.3	32.2	*33.3*	16.7	8.0	4.6	2.3	0.6	5.2
1972	580		6.0	24.3	*26.1*	25.5	11.7	4.5	1.0	0.7	0.2	4.3
1973	113		8.8	19.5	*35.4*	17.5	12.4	5.3	0.9			4.2
1974	1,024	0.2	2.8	27.7	*29.3*	21.5	13.2	4.5	0.6	0.2		4.3
1975	788		1.1	14.6	*46.3*	21.1	9.3	5.6	1.5	0.5		4.5
1967–68			0.4	4.9	30.2	31.7	15.8	9.0	5.3	2.3	0.4	5.2
1972–75		0.1	3.3	22.4	*34.2*	22.1	11.6	4.9	1.0	0.4	<0.1	4.3
1967–75		0.1	3.0	20.7	*33.8*	23.0	12.0	5.3	1.4	0.6	0.1	4.6

[a] Sample for 1967 taken from angler catch during May and June. No creel survey was conducted in that year.

greater mean length of the 1972–75 specimens (Table 4) and the generally decreasing catch per unit of effort (Table 5). The mean length of specimens in every age-class represented in the 1972–75 sample was greater than that for specimens in the corresponding year-class of the 1967–68 sample, the greatest difference (5.5 cm) being between the 3-yr-olds if the ten 9-yr-old and two 10-yr-old specimens are omitted from consideration because of smallness of the sample sizes.

Factors Affecting the Walleye Population

Undoubtedly, variable year-class strengths have contributed to the variable walleye contributions to the Lake Nipissing fishery, as Parsons (1970) noted for walleye in Lake Erie. The combination of declining contributions, increased growth rate, decreased catch per unit of effort, decreased average age and possible recruitment of sexually immature individuals, especially females (discussed below), probably coupled with a series of weak year-classes, is indicative of a rather stressed population.

The walleye population appeared to be incapable of supporting the rather intensive exploitation to which it was subjected. Its productivity and reproductive potential are probably affected by climatic factors, interactions with white suckers (*Catostomus commersoni*), northern pike (*Esox lucius*), and yellow perch, and by technology and watershed influences.

The lengthy annual freeze-up period and period of low water temperatures which occur in Lake

TABLE 4. Mean lengths of walleye of various ages in random samples from Lake Nipissing creel surveys for 1967, 1968, and 1972–75.[a]

Year	No. of fish sampled	Age (years)										Mean length (cm)
		1	2	3	4	5	6	7	8	9	10	
1967	99		23.6	25.6	31.5	35.0	39.1	43.7	45.2	46.5		35.8
1968	166		28.4	25.6	32.5	35.6	38.9	44.2	45.7	49.3	55.4	36.4
1972	580		28.4	32.8	36.8	40.6	45.2	53.6	53.6	66.0	61.1	38.4
1973	113	21.6	23.6	32.5	35.3	39.9	43.7	46.7	53.3			36.8
1974	1,024			30.5	35.0	38.4	42.2	44.7	46.5	54.5		35.8
1975	788		27.9	30.2	34.0	38.4	43.2	46.7	49.3	55.1		36.2
1967–68			29.0	25.6	32.2	35.4	39.0	44.0	45.5	48.4	55.4	36.2
1972–75		21.6	29.5	31.1	34.9	39.0	43.2	47.4	49.8	59.3	61.0	36.3
1967–75		21.6	26.2	31.0	34.7	38.6	42.7	46.8	48.3	55.2	58.2	36.5

[a]Samples for 1967 taken from angler catch during May and June. No creel survey was conducted in that year.

TABLE 5. Catches per unit of effort, summer angling, Lake Nipissing, 1960–75.[a]

Year	Total fish	Walleye	Perch	Pike	Others
1960	0.54	0.41	0.00	0.11	0.01
1961	0.41	0.28	0.03	0.10	0.00
1962	0.42	0.23	0.03	0.13	0.02
1963	0.76	0.58	0.07	0.11	0.00
1964	0.58	0.35	0.04	0.18	0.01
1965	0.59	0.32	0.05	0.15	0.08
1966	0.66	0.29		0.18	0.13
1967	—	—	—	—	—
1968	0.46	0.39	0.08	0.08	0.01
1969	0.31	0.12	0.12	0.05	0.01
1970	0.54	0.20	0.18	0.08	0.03
1971	—	—	—	—	—
1972	0.52	0.12	0.21	0.13	0.02
1973	0.43	0.28	0.34	0.13	0.03
1974	0.40	0.37	0.18	0.08	0.01
1975	0.34	0.15	0.12	0.05	0.02

[a]Number of fish caught per man-hour of angling.

Nipissing may undoubtedly restrict optimal biological activity, and hence optimal productivity, to a relatively short period of the year. Scott and Crossman (1973, p. 771) pointed out that growth of walleye is fairly rapid in the south but slower in the northern part of the range. Climatic factors, as well as limnological factors such as the relatively low mean alkalinity (24 mg/ℓ) and total phosphorus concentration (0.007–0.066 mg/ℓ) of the lake (D. D. Anthony unpublished data; Ontario Ministry of the Environment unpublished data) may therefore partly explain the lower growth rate of walleye in Lake Nipissing than in more southerly lakes (Fig. 2).

The higher growth rate of Lake Nipissing walleye during 1967–76 than before 1936 (Fig. 2), may possibly be due to reduced competition as a result of heavy exploitation, or may reflect changes which were thought to have occurred in the composition of the "walleye" population. Harkness (1936) suggested that the "walleye" of the early fishery was probably the smaller, slower-growing blue pike. The intensive exploitation of the species and the massive stocking of walleye between 1920 and 1934 may indeed have resulted in the virtual replacement of the severely depleted blue pike stock by a more vigorous, faster-growing walleye population, better adapted to the prevailing conditions.

Perhaps the single most important cause of stress in the walleye population was exploitation of fish which have never spawned or have spawned only once. Three- and 4-yr-old fish, among the most heavily exploited age-groups in the walleye fishery (Table 3), are poorly represented among the spawning stock. Annual studies conducted by the Fisheries Assessment Unit since 1969 at the Wasi Falls spawning site (the main walleye spawning site) indicate that males begin spawning at age 4 and females at age 5. Approximately 80% of the males sampled were between 4 and 6 yr old, and 87% of the females between 5 and 7 yr old. None of the females, and only 27% of the males, were 3- and 4-yr-olds (3 and 24%, respectively); so though a few 3-yr-old males did appear in the spawning runs, females did not appear until age 5.

These studies and the creel surveys further showed that females are generally between 2.5 and 5.0 cm longer than males of the same age, suggesting that females may probably enter the fishery earlier than males even though they mature later.

Interactions between walleye and other species of the fish community may also have had adverse effects on the walleye population. Increasing numbers of white suckers which use some walleye spawning sites after the walleye have spawned

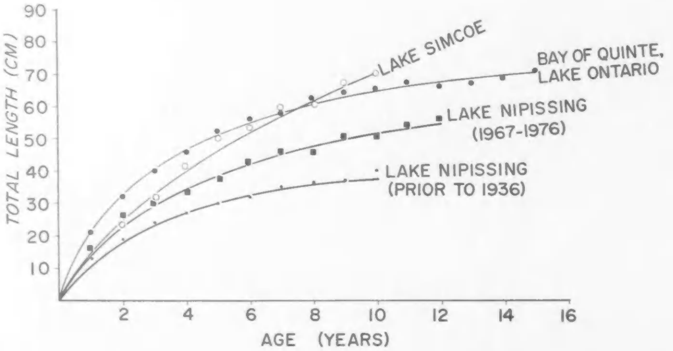

FIG. 2. Growth curves for walleye from Lake Nipissing, Lake Simcoe, and the Bay of Quinte, Lake Ontario. (Data for Lake Nipissing from Lake Nipissing Fisheries Records 1885–1976; data for the Bay of Quinte from Scott and Crossman 1971, p. 771; curve for Lake Simcoe after MacCrimmon and Skobe 1970, p. 110.)

(observations by Ministry of Natural Resources) may have interfered with development of walleye eggs, and thereby adversely affected reproduction in the population. In Lake Nipissing, the spawning periods of the two species overlap; suckers usually begin moving into the spawning areas before the walleye leave, and their spawning activities peak during the critical incubation period of walleye eggs. Scott and Crossman (1973, p. 773) regarded spawning by other species over walleye eggs as an important factor in controlling walleye populations. Because of the relatively large number of suckers using walleye spawning sites, the potential for competition and damage to walleye eggs or for excessive predation of them, appears to be real.

Similarly, competition and predation by northern pike and yellow perch may have aggravated the effects on the already stressed walleye population. Northern pike is an important competitor and probably the most important predator of walleye (Scott and Crossman 1973, p. 773), and perch compete with walleye for food, and prey on their young.

Apart from these natural interactions, two types of cultural factors have probably adversely affected the walleye fishery of the lake: those which have contributed directly to increased fishing pressure on the population and those which have created unfavourable environmental conditions for the species. Among the first type of factors are: (a) The location of the lake in the heart of the population center of northeastern Ontario, and its ready accessibility at all times of the year from all parts of the Province and beyond; (b) Improved winter access to all parts of the lake through use of snowmobiles — This has undoubtedly contributed to the increased winter fishing activities during the last decade, indicated by the marked increase in the number of ice-fishing huts on the lake during this period (from 218 in 1968 to 653 in 1976); (c) Advances in gear technology — Modern, more sophisticated gear (e.g. fishfinders, lures, etc.) was in use from the 1960s and has contributed to greater exploitation of the resource; (d) Demographic and socioeconomic factors in the immediate environs of the lake — The population of the area rose steadily during the last decade, and an even greater increase in the number of anglers on the lake was recorded over this period. Because of the generally favorable economic conditions in the area and the emphasis on recreation coupled with the increasing amount of leisure time available, more persons now own motor boats and fish the lake (for walleye) with more sophisticated gear, for longer periods than before; (e) The intensiveness of the May fishery — If size of harvest taken reflects fishing intensity, then, on the basis of the percentages of the harvest taken in each month of the open-water fisheries of 1970–75, May is the month of most intensive activity if the number of weeks of fishing is taken into account. The monthly percentages were:

	1970	1972	1973	1974	1975
May	22.0	29.3	23.7	29.3	11.6
June	34.0	34.7	44.4	37.3	50.2
July	24.0	20.0	24.2	21.0	25.0
Aug.	20.0	16.0	7.7	12.4	13.2

The data for May represent 2 wk of fishing in each of the years 1970 to 1974 and only 1 wk in 1975, compared with 4 wk for all other months.

This intensive May fishery, immediately after the walleye spawning period ends, probably harvests many fish still lingering around their spawning sites before they can move out into deeper waters; (f) The illegal and the Indian fisheries, whose annual combined harvest is estimated to be equivalent to about 25% of the legal angler harvest — As the estimated total angler harvest for 1972 (Table 2) was approximately 300,000 kg, the unrecorded fisheries are presumed to have harvested about 75,000 kg in that year alone. For years, Indians from Nipissing Reserve Number 10 (Fig. 1) were gillnetting walleye for sale to various outlets in the Province. The information now available suggests that the magnitude of this Indian fishery may be even greater than previously thought, and so must have an effect on the walleye stock.

The second type of cultural factors include loss or deterioration of walleye spawning areas due to such watershed influences as industrialization, urbanization, and shoreline development.

The effect of industrialization is especially well documented for the Sturgeon River and Duchesney Creek, two of the larger inlet streams of the lake (Fig. 1). Both streams were lost as major walleye spawning sites as a result of industrial pollution. Since the Abitibi Forest Products mill went into operation in 1928 at the town of Sturgeon Falls, the Sturgeon River rapidly deteriorated as a spawning site due to accumulations of bark and pulp wastes on the river bed (Mackay 1930; Ontario Ministry of the Environment unpublished data). Walleye have long since ceased spawning up the river. Similarly, after the Canadian Johns-Manville Paper Products plant began operation in the city of North Bay in 1956, walleye ceased spawning in Duchesney Creek, into which untreated effluents were discharged, and along the nearby shoreline of the lake, as a result of water quality and spawning site impairment (Ontario Ministry of Natural Resources unpublished reports).

Though most of the lake's extensive watershed (12,300 km^2) remains forested or rural and undeveloped, urbanization and shoreline development to recreational and residential functions have greatly increased since the Second World War, especially during the last decade. Shoreline development has been most extensive in the south-shore area; and since 1968 urban expansion has been especially rapid in the city of North Bay, which occupies most of the eastern shoreline, as well as the drainage basin of three of the largest inlet streams. There is evidence that accelerated erosion and silting attributable to such developments have had adverse effects on spawning sites in some parts of the system (Fisheries Assessment Unit Spawning Site Study 1973; D. D. Anthony unpublished report).

Various measures aimed at minimizing and/or reversing environmental damage were implemented with measurable degrees of success in some cases. Treatment and recycling of effluents, and other corrective measures instituted at the Johns-Manville plant, have resulted in improvements in Duchesney Creek, including a return from a pH of 4 to a normal pH of 7 downstream of the plant. As a result, since the spring of 1973, walleye have been returning to the creek to spawn. The results of a spawning site rehabilitation program begun in 1973 seem promising and, with the recently completed installation of pollution control facilities at the Abitibi plant, comes the promise of eventual reclamation of the Sturgeon River as a major walleye spawning area.

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Population Dynamics of Percids in Lake IJssel and some Smaller Lakes in The Netherlands[1]

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WILLEMSEN, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710–1719.

Pikeperch (*Stizostedion lucioperca*) and Eurasian perch (*Perca fluviatilis*) in Lake IJssel both prey mainly upon the very abundant smelt (*Osmerus eperlanus*). But competition for food is of little or no importance and growth is not density-dependent. Growth rates for perch and ruffe (*Gymnocephalus cernua*) in some lakes are exceptionally rapid, mean lengths after 3 yr being 24 and 18 cm, respectively. Very intensive fishing for pikeperch (total annual mortality 81%) in the season before first spawning removes particularly the fast-growing fish from the population, thus restricting reproduction mainly to the slow-growing pikeperch. Year-class strength of pikeperch is strongly favored by a high summer temperature during the first year of life. Strong year-classes of pikeperch in Lake IJssel are characterized by a mean length of the young-of-the-year of 14.5 cm or more. Migration of pikeperch and perch in Lake IJssel is restricted. When transported to other areas of the lake, both species showed a distinct homing behavior.

Key words: Percidae, population dynamics, *Stizostedion*, *Perca*, *Gymnocephalus*

WILLEMSEN, J. 1977. Population dynamics of percids in Lake IJssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710–1719.

Le sandre (*Stizostedion lucioperca*) et la perche eurasienne (*Perca fluviatilis*) du lac IJssel se nourrissent tous deux surtout d'éperlans (*Osmerus eperlanus*), qui sont très abondants. La concurrence alimentaire n'a cependant que peu ou pas d'importance, et la croissance ne dépend pas de la densité. Le rythme de croissance de la perche eurasienne et de la perche goujonnière (*Gymnocephalus cernua*) dans certains lacs est exceptionnellement rapide, les longueurs moyennes après trois ans étant de 24 et 18 cm respectivement. Une pêche très intensive du sandre (mortalité annuelle totale de 81%) pendant la saison qui précède la première fraie retire de la population les poissons dont le rythme de croissance est particulièrement rapide, limitant ainsi la reproduction en grande partie aux sandres à croissance lente. Des températures estivales élevées durant la première année de vie contribuent beaucoup à l'abondance d'une classe d'âge de sandres. Les fortes classes d'âge de sandres dans le lac IJssel sont caractérisées par une longueur moyenne des jeunes de l'année de 14.5 cm ou plus. La migration du sandre et de la perche eurasienne dans le lac IJssel est limitée. Transportées dans d'autres régions du lac, les deux espèces exhibent un comportement distinct de homing.

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To provide a better base for the management of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*), research has been carried out by the Netherlands Institute for Fishery Investigations since 1936 on feeding, growth, reproduction, year-class strength, migration, and mortality of these two species. Some aspects of the biology of ruffe (*Gymnocephalus cernua*), a prey fish of perch and pikeperch, were studied also. This paper reviews briefly some of the more important results of the investigations. Where the information is not referenced to a previous publication, the data and observations are from my unpublished material.

The total area of the Netherlands (32,450 km^2) includes 1300 km^2 of lakes, rivers, canals, and brooks and another 1200 km^2 in Lake IJssel (IJsselmeer). With some exceptions these waters are shallow, eutrophic, and, especially the larger ones, rather turbid (Table 1). Eel (*Anguilla anguilla*), pikeperch, perch, and pike (*Esox lucius*) are important to the commercial fishery. Sportfishing, which is practiced by about 10% of the Dutch population, is aimed at a much greater diversity of species.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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Research on percids has been concentrated mainly on Lake IJssel which was formed in 1932 when the enclosure dam was completed and the Zuiderzee changed from a marine bay into a lake (Fig. 1). Freshwater is supplied to Lake IJssel by the River IJssel, a tributary of the River Rhine. Chlorinity decreased rapidly and in 1936–37 reached the present level of 200–250 mg/ℓ (Havinga 1941). Freshwater fish from some coastal areas and river mouths invaded the lake, and about 1936 a population had been established (Havinga 1945) much like the one in 1975. The original area of Lake IJssel, 3600 km^2, was reduced step by step by the building of three enclosure dams and subsequently pumping out the water. In 1975 the area was 2000 km^2, but the recent construction of a final dam reduced it to 1200 km^2.

Since 1970, fishing with the eeltrawl has not been allowed in Lake IJssel because of the high mortality of young pikeperch and perch. The effects upon the catch were considerable, especially for fish of low value, mainly ruffe, smelt (*Osmerus eperlanus*), bream (*Abramis brama*), and roach (*Rutilus rutilus*). At the same time the catches ($kg \cdot ha^{-1} \cdot yr^{-1}$) of pikeperch and perch more than doubled:

Period	Pikeperch	Perch	Eel	Other species
1949–69	1.9	0.8	9.9	38.1
1970–75	3.5	2.4	4.6	4.4

The average catch of pikeperch in Lake IJssel roughly equals the catch in many other typical pikeperch lakes in Europe, but is far below the maximum in some bays along the Baltic Sea (mean catch 11.4 $kg \cdot ha^{-1} \cdot yr^{-1}$, Schlumpberger 1976).

The annual catch of perch increased continuously from 0.7 $kg \cdot ha^{-1}$ in 1970 to 4.0 in 1975. This catch is rather high in comparison with most other perch lakes, but considerably lower than the maximum of 11.9 $kg \cdot ha^{-1} \cdot yr{-1}$ in Germany (Tesch 1955). Considering the favorable environmental conditions and the abundance of prey fish in Lake IJssel, the catch of pikeperch and perch seems to be much lower than the potential catch. Ruffe is abundant in the larger lakes but of no interest for the sport or the commercial fishery. It possibly competes for food with bream and eel, and is an important prey fish for larger perch and pikeperch.

Food

The main conclusions about the food of pikeperch and perch in Lake IJssel are: (a) there is, despite some minor differences, a striking similarity in feeding (concerning both size and species of prey), and (b) predation within and between these species is very restricted. Pikeperch and perch feed first mainly on Rotifera (Belyi 1972; Brezeanu 1972) or nauplius larvae, and after several days on an increasing proportion of adult copepods (Rogowski and Tesch 1961; Willemsen 1969). The frequencies of occurrence (%) of food organisms in the stomachs of pikeperch and perch 6–10 mm long in Lake IJssel indicate that the two species start feeding on zooplankton of nearly identical compositions, both qualitatively and quantitatively:

Species	Rotifera	Nauplius larvae	Copepodids	Adult copepods	Cladocerans
Pikeperch	8	37	78	41	36
Perch	3	52	85	37	10

Stomach contents of postlarval pikeperch and perch caught mainly in trawl nets during 1966–76 in Lake IJssel (Table 2) indicated that:

a) Up to a length of 5 cm, zooplankton are the main food, supplemented by chironomid larvae.

b) The main transition food organisms between zooplankton and fish are *Neomysis* and *Gammarus* spp. (the latter for perch only).

c) Fish predominate in the diet of pikeperch over 5 cm and of perch over 10 cm. In many

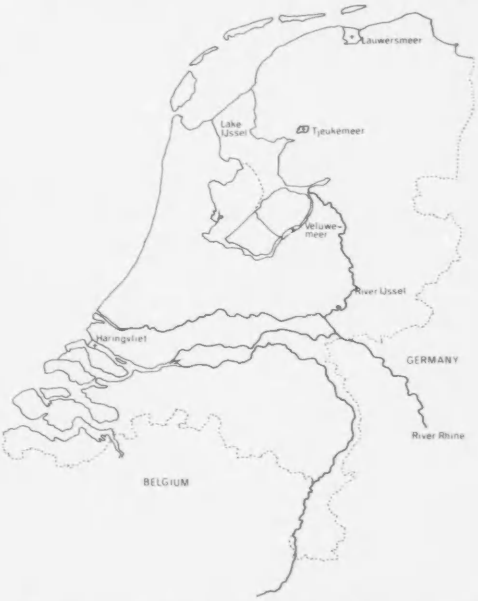

FIG. 1. Lakes in the Netherlands mentioned in this paper.

TABLE 1. Physicochemical characteristics of Lake IJssel (partly from de Kloet 1971 and Anon. 1976).

Area (km^2)	1980 (since 1975, 1200)
Depth (m), mean	4
maximum	10.2
Bottom	sand and clay
Average residence time (mo)	6–9
Water temperature (°C), mean	10.4
maximum	24.5
Transparency (Secchi disc, m)	0.65 (0.1–2.0)
pH, winter/summer	7.5–8.0/8.2–8.7
Oxygen saturation (%)	90–120
P–P$_{tot}$ (mg/ℓ)	0.22
N–N$_{tot}$ (mg/ℓ)	4
Cl (mg/ℓ)	220
Primary production, entire year (g·cm^{-2}·day^{-1})	2

TABLE 2. Frequencies of occurrence (percentages of fish with full stomachs) of items in stomachs of pikeperch and Eurasian perch of various sizes from Lake IJssel, 1966–76. (Other fish = other species and unidentified fish remains).

			Invertebrates				Fish					
Length group, cm	Total number	% empty	Zooplankton	Chironomids	*Neomysis* spp.	*Gammarus* spp.	Smelt	Ruffe	Cyprinids	Pikeperch	Perch	Other fish
						Pikeperch						
2– 5	219	8	83	8	2	—	18	—	—	—	—	2
6–10	336	35	1	—	15	—	83	—	—	—	—	1
11–20	699	36	—	—	3	—	95	2	1	—	—	—
21–30	329	38	—	—	1	—	89	8	1	—	—	2
31–40	577	39	—	—	—	—	88	14	1	—	0.3	—
41–50	615	34	—	—	—	—	92	14	3	0.3	1	—
51–90	148	47	—	—	—	—	58	38	19	—	—	1
						Perch						
1– 5	64	0	95	22	2	—	—	—	—	—	—	—
6–10	182	41	40	—	11	38	20	—	—	—	—	—
11–15	281	38	5	1	19	10	75	1	—	—	—	1
16–20	308	51	1	—	7	3	84	6	—	—	—	4
21–25	473	53	—	—	3	1	80	20	—	—	0.5	3
26–30	398	54	—	—	1	2	70	24	—	—	2	3
31–45	404	61	—	—	—	—	61	75	—	—	6	1

other waters, Eurasian perch start preying on fish at a length of about 15 cm (e.g. Röper 1936; Deelder 1951; Bauch 1963), but Holčik (1969), Hartmann (1975), and Chikova (1970) found that fish predominated in the food of perch at minimum lengths of 20, 26, and 26–28 cm, respectively. According to Klemetsen (1973) in a Norwegian lake, perch even larger than 30 cm still preyed mainly on benthic invertebrates.

d) Smelt is the most important food fish and may, as its relative abundance in the stomach contents is higher than in the population, be considered the preferred food. Only for the large predators, which form a small part of the total population, do ruffe and cyprinids (bream and roach) reach the same level of importance as smelt. In Tjeukemeer, where smelt are abundant, this species is the main food item, but in Veluwemeer, where smelt are scarce, cyprinids and ruffe are the main food (Table 3). Furthermore, invertebrates appear to be of importance as food in Veluwemeer and Lauwersmeer, that is, for pikeperch *Neomysis* spp., and for perch a group of various organisms (*Neomysis* spp., chironomid larvae, *Gammarus* spp., and zooplankton). The considerable differences in diet

TABLE 3. Frequencies of occurrence (percentages of fish with full stomachs) of items in stomachs of pikeperch (>11 cm) and perch (>15 cm) in three lakes.

	Number	Invertebrates	Smelt	Ruffe	Cyprinids	Pikeperch	Perch	Other fish
			Pikeperch > 11 cm					
Veluwemeer	191	18	4	25	49	4	2	—
Lauwersmeer	130	51	32	12	2	3	—	5[a]
Tjeukemeer	112	—	96	4	2	—	1	—
			Perch > 15 cm					
Veluwemeer	81	43	1	23	33	—	—	—
Lauwersmeer	76	84	3	5	1	—	1	13
Tjeukemeer	20	—	70	20	—	—	5	5

[a]Mainly threespined stickleback (*Gasterosteus aculeatus*).

between fish of these lakes demonstrate that the food choices are rather flexible, availability being more decisive than preference. This conclusion is strengthened by reports of a variety of species as main prey for pikeperch: smelt (Neuhaus 1934; Havinga 1945), cyprinids (Horoszewicz 1964), perch and pikeperch (Nagięć 1966), and ruffe (Biró 1971); and for perch: cyprinids (Horoszewicz 1964; Banks 1970), smelt and ruffe (Havinga 1945), and cyprinids and perch (Dziekonska 1954).

e) Cannibalism among pikeperch over 11 cm is only 0.14%, prey fish being very abundant. In Veluwemeer, where prey fish are less abundant, cannibalism was 4% in years with high abundance of young pikeperch. Perch over 15 cm in Lake IJssel have a higher percentage (2%) than pikeperch and here cannibalism distinctly increases with length. In waters where young of the same kind are abundant, and other prey fish scarce, cannibalism may occur frequently, as is shown for pikeperch in Lake Balaton (frequency of occurrence 30%), by Biró and Elek (1969) and for perch in Polish lakes (36%) by Dziekonska (1954). In such situations cannibalism may have serious implications for year-class strength.

f) Predation of pikeperch on perch, and the reverse, is negligible.

The maximum prey length consumed by pikeperch and perch amounts to nearly 50% of the predator length (Steffens 1960; Popova 1966; Willemsen 1969), but generally these fish take small prey. In Lake IJssel the mean lengths of prey fish of pikeperch are only slightly greater than for prey of perch of the same size, the mean prey lengths (cm) for various length groups of pikeperch and perch being:

	Length group of predator (cm)						
Predator	11–15	16–20	21–30	31–40	41–50	51–60	61–70
Pikeperch	5.8	6.3	7.5	8.1	8.5	9.0	9.7
Perch	5.1	6.1	6.9	7.4			

These data also show that, as for walleye (*Stizostedion vitreum vitreum*) (Parsons 1971), the size of the prey in relation to that of the predator decreases with increasing length of the predator. It decreased for pikeperch within the length range 11–70 cm from 45 to 15%, and for perch of 11–40 cm from 39 to 21%.

The food of the ruffe in lakes IJssel and Lauwersmeer consists mainly of *Gammarus* spp. and chironomids.

Growth

In Lake IJssel, food shortage probably does not inhibit growth of either pikeperch or perch. Although these species are potentially food competitors, there is little or no inter- or intraspecific competition. At the present population level, growth of these species is not density-dependent, which means that the productive capacity of Lake IJssel is probably utilized insufficiently.

Different methods of ageing have been tested. The criteria were the correctness of age readings from returned tagged fish and the requirement that exceptional strong year-classes could be followed in the population during a number of years. Most reliable results were obtained with finrays for perch (methods described by Chugunova 1963 and Deelder and Willemse 1973) and with scales for pikeperch. The latter method provided correct age readings for 98% of the returned pikeperch.

Growth of pikeperch was determined, besides by direct aging, by back-calculating from scales, using Lea's formula: $L_n = S_n/S\ (L–C) + C$, where S_n and S are the equivalents for anterior scale radii at time of annulus formation and of capture, respectively, and L_n and L the corresponding fish lengths. Measurements of scales and total lengths of pikeperch in Lake IJssel provided for the correction factor, C, a value of 4.9.

Growth rates of percids in the Netherlands is intermediate between those reported in other European countries (Table 4). In the colder parts of its distribution, pikeperch grows rather slowly,

TABLE 4. Lengths at various ages (yr) of three percids in some lakes (IJssel, 1966–76; Lauwersmeer, 1972–76; Haringvliet, 1973–75) in the Netherlands compared with rapid and slow growth rates in other countries.

			Total length (cm) at age					
Water	Country	Author	1	2	3	4	5	6
Pikeperch								
Lake IJssel	Netherlands		15	30	42	50	57	63
Lauwersmeer	Netherlands		11	26	39	48		
Tjeukemeer	Netherlands	Willemsen 1969 van Zalinge 1970	13	28	40	45		
Upper Ob	USSR	Solovov 1971	17	35	50	63	72	
Lake Balkhash	USSR	Solovov 1971	24	42	55	61	67	
Lake Mermere	Turkey	Aksiray 1960	23	31	47	58		
Lower Vistula	Poland	Nagięć 1964	17	29	45	58	68	77
Mälaren	Sweden	Svärdson and Molin 1973	11	20	29	34	39	45
Perch								
Lauwersmeer	Netherlands		10	19	24	30		
Haringvliet	Netherlands		10	17	23			
Lake IJssel	Netherlands		8	15	21	26	29	31
Lake Constance	W. Germany	Haakh 1929		16	21	25	27	31
Lake Constance	W. Germany	Hartmann 1975		16	20	22		
25 lakes	W. Germany	Bauch 1963	7	11	14	16	18	20
Dubh Lochan	Scotland	Shafi and Maitland 1971	5	8	9	11	12	
Ruffe								
Lauwersmeer	Netherlands		8	15	18	19		
Lake IJssel	Netherlands		6	9	10	11		
Zalew Wislany (Vistula Firth)	USSR/Poland	Neuhaus 1934 Nolte 1939	8	12	14	16		
23 lakes	W. Germany	Bauch 1963	6	9	11	12		

but at high temperatures growth rate may be rapid, reaching its maximum in central Asia. The mean length attained in Lake IJssel after 4 yr was 50 cm compared with 42–50 cm for nine other Dutch lakes with nearly equal temperatures. The relatively small differences in growth between these lakes strongly suggest that the fastest growth, such as in Lake IJssel, approaches the maximum value in this climate. Growth retardation in some of these lakes is probably due to insufficient availability of prey fish.

Growth of perch in Lake IJssel is extremely rapid, but is surpassed by that in Lauwersmeer and Haringvliet. The last two waters are exceptional in that they were originally marine and became freshwater basins, after enclosure by dams in 1969 and 1970, respectively. The initial environmental conditions in these new lakes were apparently extremely favorable for perch because of a very abundant food supply (Steinmetz 1975).

In a number of respects, the growth patterns of pikeperch and perch are similar. Females grow slightly faster than males. In Lake IJssel females at age 6 are 3 cm (pikeperch) or 2 cm (perch) larger than males.

Growth rate can be high even if the preferred food is insufficiently available. Though rapid growth of pikeperch in Baltic Sea embayments is ascribed to the presence of numerous smelt (Wiktor 1961), this species is not a prerequisite for rapid growth; the growth rate in Veluwemeer (smelt scarce) is exactly the same as in Lake IJssel (smelt abundant). According to some authors (Deelder 1951; Tesch 1955; Holčik 1969; Ilina 1970; Sumari 1971) the growth rate of perch larger than about 15 cm is inhibited if sufficient prey fish are unavailable. But comparison of excellent growth in Lauwermeer, where perch 16–30 cm long feed mainly on invertebrates with the growth in Lake IJssel, where perch prey mainly on fish, shows that abundance of invertebrates may result in as rapid growth as abundance of fish. A comparable situation of fast growing perch feeding to a large extent on invertebrates exists in Lake Constance (Hartmann 1975).

The growth rates of percids are practically constant and bear little negative relation to density. In Lake IJssel the population density fluctuates considerably, the ratio between highest and lowest catch amounts to approximately 10 for perch and 50 for pikeperch. Some very strong pikeperch year-classes such as 1937 (Havinga 1945), 1969, 1970, and 1973 and the recent strong perch year-classes grew even slightly faster than the average.

In the commercial fishery, mainly the larger individuals are caught from the recruiting year-classes. For example, the mean length of 4-yr-old perch from Lake IJssel in 1972–74 was 28.1 cm in samples from catches in commercial trammel nets, but only 25.4 cm in small-meshed trawlnet surveys. In recent commercial catches the mean length of 3-yr-old pikeperch was 43.5 cm but survivors caught as 4-yr-old fish appeared from back calculations to have been only 37.5 cm at age III. This implies that reproduction of pikeperch in Lake IJssel is mainly restricted to slow growing fish. The fishery also crops fast-growing perch, but as spawning has occurred before recruitment age, the spawning stock consists of both fast and slow growing individuals and hence there is less chance for possible genetic deterioration with this species.

The growth rate of ruffe in Lake IJssel is, as in most Dutch waters (Bouwman personal communication), low. Data from Lauwersmeer show, however, that in the Dutch climate much faster growth is possible. It is remarkable that in this lake the benthos-feeding ruffe and the benthos- and fish-feeding perch both grow at a rate which is nowhere else equaled in Europe, whereas the exclusively fish-feeding pikeperch shows an average growth.

Reproduction

In waters where pikeperch and perch grow fast, maturity is attained in general 1–2 yr earlier than in those where growth rate is low. The lengths (cm) and ages (yr) at which 50% of the males and females of pikeperch and perch and 50% of ruffe reach maturity in Lake IJssel, as follows, correspond with data for waters with good growth (Filuk 1962; Tesch 1955):

	Pikeperch		Perch		Ruffe
	♀	♂	♀	♂	
Length	40	26	20	15	6.5–7
Age	3	2	3	2	1

Fecundity varies widely in pikeperch (Deelder and Willemsen 1964) and perch (Bauch 1963; Craig 1974). The following data show fecundities in Lake IJssel for pikeperch and perch which are average according to the above studies, and that relative fecundity is not length-dependent in perch but increases with length in pikeperch, at least up to 55 cm:

	Pikeperch				Perch			
Length, cm	40	45	50	55	22	25	28	31
Eggs × 10^3	60	120	240	350	28	45	63	87
Eggs/g fish	109	152	211	222	200	200	194	198

Percids in Lake IJssel spawn mainly during April (perch), late April and early May (pikeperch) and May–June (ruffe) at temperatures of about 8–12, 11–15 and 12–18°C, respectively.

Year-Class Strength

Strong year-classes of pikeperch appear to be related to high summer temperatures and fast growth. From 1966 to 1975 the strongest pikeperch year-class in Lake IJssel was, at the age of recruitment to the fishery, about 20 times as abundant as the weakest one (Table 5). The ratio for perch was considerably more than 100.

Larval abundance is not an infallible predictor of ultimate year-class strength of pikeperch and perch. Mortality after the larval stage, but before the end of the summer, is mainly responsible for the considerable fluctuations in year-class strength: Spearman's rank correlation coefficients between abundance of larvae and commercial catch were not significant for pikeperch (0.61) and perch (0.09) but were significant between abundance of age-group 0 and catches for both pikeperch and perch (0.86, $P < 0.01$).

In the Netherlands, high temperature during the summer appears to have a positive effect on year-class strength of pikeperch. In Lake IJssel, the 10 strongest pikeperch year-classes from 1936 to 1975 occurred in years when the mean water temperatures during June–August were 0.5–1.0 deg. C higher than in those years which produced the 10 weakest year-classes. Temperature during the spawning season, however, was about 1 deg. C lower for the strong year-classes than for the weak ones.

Correlations were calculated for pikeperch between the sum of the day-degrees above 14°C for 1966–75 (Table 5) and both the number of young-of-the-year pikeperch taken per hour trawling and the number in the catch. Both these correlations were significant [$r = 0.80$ ($P < 0.01$) and 0.84 ($P < 0.01$), respectively], in contrast to nonsignificant correlations between year-class strength and mean monthly temperatures. Thus it is not high temperature during any specific month but a high temperature during the whole summer which favors year-class strength.

TABLE 5. Various measures of year-class strengths of pikeperch and perch in Lake IJssel, 1966–75.

		Pikeperch			Perch			
Year-class	Day-deg. >14°C	Larvae per 100 m[a]	Age-group 0 per hour[b]	Catch $\times 10^3$[c]	Larvae per 100 m[a]	Age-group 0 per hour[b]	Age-group 1 per hour[b]	Catch $\times 10^3$[c]
1966	531	5	100	368	—	—	—	—
1967	392	10	71	286	16	18	10[d]	58
1968	432	7	91	109	36	25[d]	5	5–10
1969	556	16	383	1609	84	451	273	1379
1970	481	17	608	913	91	387	144	917
1971	482	11	100	418	120	269	107	419
1972	367	3	26	116	122	5	5	19
1973	533	6	349	1322	179	235	116	477[d]
1974	389	22	52	102[d]	105	501	140	—
1975	568	36	365	—	522	3349	1028	—

[a] Mean number per 100 m tow for 4–8 samples at 14 stations.
[b] Mean number caught per hour trawling at end of first summer and data from Steinmetz and Oudelaar (1971).
[c] Calculated total number of fish in commercial catch; for pikeperch at age II, for perch at age III.
[d] Number estimated.

As high temperatures during the summer result as well in faster growth, young-of-the-year pikeperch of strong year-classes should be larger than the average. That this was true was demonstrated for the 17 yr for which data were available on year-class strength and mean lengths of young-of-the-year pikeperch (partly derived from Havinga 1945). Year-class strength was classified as strong or weak on the basis of both the abundance of young-of-the-year and the catch of age-group II. Of year-classes with young-of-the-year averaging 11–14.4 cm, seven out of eight, were weak; of those with the fish averaging 14.5–18 cm, all were strong. In Lake IJssel, length-dependent winter mortality of pikeperch was not responsible for the fluctuations in year-class strength, in contrast with the findings by Svärdson and Molin (1973) for pikeperch in Sweden and by Chevalier (1973) for walleye in Oneida Lake, New York. Length-dependent mortality during the winter should be recognizable by an increase in mean length, given the fact that during this period growth comes to a standstill. Furthermore, this increase should be especially large for weak year-classes. Of eight pikeperch year-classes in Lake IJssel for which mean lengths were determined just before and after the winter, the increases for the four strong year-classes were 0, −0.5, 1.3, and 0.1 cm and those for the weak ones were 0.2, 0.2, 0.4, and 0 cm. These small increases (and decrease) were probably caused by sampling errors, and showed no relation to length-dependent mortality. This conforms to the earlier conclusion that year-class strength is established before the winter.

Perch showed much smaller differences in growth rate during the first year than pikeperch and the differences could not be connected with the considerable variations in year-class strength. Data from 10 year-classes indicated that mean lengths over 8 cm occurred only in strong year-classes but that two very strong year-classes had attained mean lengths of only 7.0 and 7.2 cm.

Of other possible factors in year-class strength, none of the following appeared to apply for pikeperch and perch in Lake IJssel: for perch, sum of day-degrees above 14°C (Le Cren 1958); for perch and pikeperch, cannibalism (Alm 1951; Chevalier 1973), interspecific predation (Negonovskaya 1971; Forney 1973), abundance of suitable zooplankton (Rogowski and Tesch 1961), and changes in water level during spawning period (Svärdson and Molin 1973); for pikeperch, wind-direction and -force during spawning (Woynarovich 1960, 1963), and time lapse between spawning of smelt and pikeperch (Neuhaus 1934).

Migration

The majority of pikeperch and perch in Lake IJssel do not migrate extensively. Information about the extent of migration was obtained from a tagging program carried out in 1969–75. Large numbers of pikeperch and perch were tagged with Floy anchor tag FD-67 and released (Table 6) in the northern and southern halves of Lake IJssel. The recapture data on fish returned from known locations indicated as follows:

a) Of the pikeperch caught and released in the northern half, 80% were recovered from the same area; of those caught and released in the southern part, 93% were recovered from the same area; of those caught in the northern half and released in the south, 69% were recovered

TABLE 6. Percentages of tagged pikeperch and perch recaptures from known locations in north and south parts of Lake IJssel, 1969–75, after being taken and released in one or other of the two areas.

Area of				% of recaptures from known locations in	
Catch	Release	Number tagged	Percent recaptured	North	South
		Pikeperch			
North	North	1358	23.0	76.6	18.6
South	South	565	26.5	6.7	84.7
North	South	133	22.6	60.0	26.7
		Perch			
North	North	4149	24.7	69.3	6.6
South	South	1818	18.4	8.4	55.8
North	South	2013	10.7	43.3	27.0

TABLE 7. Total annual mortalities of age-II and age-III pikeperch in Lake IJssel, in various years, 1966–74.

Year-class	Number ($\times 10^3$) in catch			Total mortality, %	
	Age II	Age III	Age IV	II–III	III–IV
1966	368	81	13	78	84
1967	286	56		80	
1968	109	23		79	
1969	1609	131	19	92	85
1970	913	227	16	75	93
1971	418	55		87	
1972	116	30		74	
1973	1322	202		85	
1974	102				

from the northern part; the migratory behavior of perch was similar to that of pikeperch.

b) It appears that most pikeperch remain in their original areas for years; during the first year 81% of the recaptures came from the original area and this percentage changed only slightly during the following 3 yr (77%). Migration of perch was even more limited; during the first year 92% of the recaptures came from the original area and in the next 3 yr also 92%.

c) Pikeperch and perch show a tendency for homing. The majority of the recoveries of pikeperch caught in the northern half and released in the south came from the northern part. Perch also were mainly recaptured in the northern half after transportation from north to south.

d) Only 1.5% of the pikeperch and 0.7% of the perch were recaptured outside Lake IJssel, and then nearly all from the River IJssel not far upstream.

Mortality

Total mortality of pikeperch in Lake IJssel, calculated from the decrease in numbers of a year-class in the commercial catch of succeeding years from 1966 to 1974 (Table 7), averaged 81% during the third year of life. (Numbers for age IV were omitted when this group was represented in the samples by such small numbers that no reliable total could be calculated.) Fishing intensity remained fairly constant during the period, therefore the numbers in the commercial catch were largely representative for the total population of pikeperch of the age-groups concerned. Total mortality during the fourth year could be calculated for three year-classes only, so the mean value of 87% is little more than an estimate.

Total annual mortality of pikeperch was also determined by totalling recaptures of tagged pikeperch according to the time elapsed since tagging. The numbers returned during the first, second, and third years after tagging were 567, 69, and 15, respectively. If tag losses and mortality due to tagging are assumed to be restricted to an initial period of 1 or 2 mo at most, this decline in numbers is a measure for total mortality, which for the two intermediate periods amounted to 88 and 78%, respectively. This confirms the above calculation of 81%.

Total annual mortalities for perch in Lake IJssel, calculated from age IV to V decreases in the commercial catch of two year-classes, were 67 and 52%. From recaptures of tagged perch, a total mortality of 58% per year was calculated. Natural mortality of young perch in Lake IJssel has been calculated from the difference in numbers caught in trawl nets during the autumn of the first and second year of life (Table 5). For six year-classes (1969–75, except 1972) natural mortality during the second year averaged 59%, which is an overestimate, because in the calculation it is assumed that the catchabilities of age 0 and age I are equal. Net avoidance will, however, be higher in the older age-group, so annual natural mortality will certainly be less than the calculated 59%. The same applies to the percentages of 64–65 calculated by Holčik (1969) for perch in Czechoslovakia.

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Trends in Harvests of Pikeperch (*Stizostedion lucioperca*), Eurasian Perch (*Perca fluviatilis*), and Northern Pike (*Esox lucius*) and Associated Environmental Changes in Lakes Mälaren and Hjälmaren, 1914–74[1]

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RUNDBERG, H. 1977. Trends in harvests of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and northern pike (*Esox lucius*) and associated environmental changes in lakes Mälaren and Hjälmaren, 1914–74. J. Fish. Res. Board Can. 34: 1720–1724.

The fish communities in and the trophic states of lakes Mälaren and Hjälmaren have changed gradually since the late 1700s. In both lakes, pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and northern pike (*Esox lucius*) are important species in the recreational and commercial fishery. Pikeperch has increased from an unimportant species to predominance in both lakes. The importance of Eurasian perch however, has decreased markedly. The most likely explanation for these changes is increased cultural eutrophication.

Key words: Percidae, pikeperch, Eurasian perch, northern pike, harvests, eutrophication, community change, behavior

RUNDBERG, H. 1977. Trends in harvests of pikeperch (*Stizostedion lucioperca*), Eurasian perch (*Perca fluviatilis*), and northern pike (*Esox lucius*) and associated environmental changes in lakes Mälaren and Hjälmaren, 1914–74. J. Fish. Res. Board Can. 34: 1720–1724.

Depuis la fin des années 1700, les communautés de poissons et l'état trophique des lacs Mälaren et Hjälmaren ont changé graduellement. Dans les deux lacs, le doré bleu (*Stizostedion lucioperca*), la perche eurasienne (*Perca fluviatilis*) et le grand brochet (*Esox lucius*) sont d'importantes espèces de sport et de commerce. D'espèce peu importante, le doré bleu a augmenté et est devenu prédominant dans les deux lacs. L'importance de la perche eurasienne, cependant, a diminué notablement. L'explication la plus probable de ces changements est une eutrophisation agricole accrue.

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THE fish communities and trophic states of lakes Mälaren and Hjälmaren have changed gradually since the 1700s. The changes in landings of three important fish species (pikeperch, *Stizostedion lucioperca*; Eurasian perch, *Perca fluviatilis*; and northern pike, *Esox lucius*) are examined, especially in relation to associated environmental changes.

Lake Mälaren is a series of basins connected by shallow sounds, whereas Lake Hjälmaren has more open areas (Fig. 1). As a result, Lake Mälaren, with less exposed shoreline, has larger areas covered by reeds and other aquatic plants. Most of the shoreline in the central basin of Lake Hjälmaren is too exposed for vegetation.

Situated in a densely populated area in southern Sweden, the lakes were subjected to increasing eutrophication from about 1900 to 1969–70, when improved sewage treatment was implemented with 90% phosphorus reduction effective in an increasing number of treatment plants. In 1976 all communities with populations > 200 were to have sewage treated to 90% reduction (Ahl 1975). Mälaren is more eutrophic in the western and northern bays, whereas Hjälmaren is more polluted in the very shallow western bays (Ahl and Willén 1970). The eastern and northern parts of Mälaren stratify during the summer. Hjälmaren does not stratify at all. Physicochemical data in Table 1 are mean values for May–August and only for the open parts of the lakes.

There are no official statistics for the freshwater fishery in Sweden. However, reliable statistics for the commercial fishery are available for Mälaren from 1964 and for Hjälmaren from 1966. Landings for the 1914–23 period from the entire lakes and some local statistics are also available but are not considered entirely reliable.

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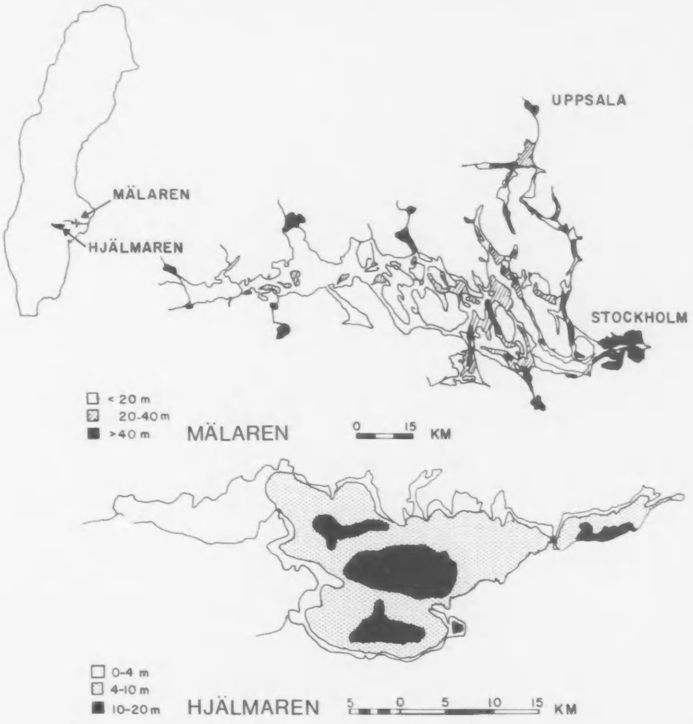

FIG. 1. Bathymetry of lakes Mälaren and Hjälmaren.

TABLE 1. Some physicochemical data for lakes Mälaren and Hjälmaren.

Characteristic	Mälaren	Hjälmaren
Drainage area (km^2)	22603	4053
Lake area (km^2)	1140	484
Altitude (m)	0.3	21.9
Max depth (m)	61	20
Avg depth (m)	13	6.1
Retention time (yr)	2.8	3.7
Transparency		
Secchi disc (m)	3.5	2.2
pH	7.5	7.5
Total N ($\mathrm{mg \cdot l^{-1}}$)	0.75	0.71
Total P ($\mathrm{mg \cdot l^{-1}}$)	0.038	0.044
Conductivity 20°C ($\mathrm{mS \cdot m^{-1}}$)	17.0	19.0
Chlorophyll *a* ($\mathrm{mg \cdot m^{-3}}$)	11	26

Fishing Methods

Gear used in the pikeperch fishery includes gill nets and trap nets in both lakes and trawls in Lake Hjälmaren. Gill nets are used in spring, fall, and winter and take approximately 75% of the catch in both lakes. Trap nets are used during the ice-free period with best catches in spring in Mälaren and in spring and early fall in Hjälmaren. Although limited trawling has been done in the late fall in Hjälmaren, this gear has never been successful. Large by-catches of bream (*Abramis brama*), white bream (*Blicca bjoerkna*), and roach (*Rutilus rutilus*) hinder the efficiency of using this gear for preferred species.

Fyke nets are used to capture northern pike during the spawning season. Gill nets are used during the remainder of the year. Approximately one third of the total northern pike catch is taken in fishing for pikeperch.

Eurasian perch is a by-catch in the commercial fishery for pikeperch and eel (*Anguilla anguilla*). Trap nets in Hjälmaren, with smaller mesh sizes than those used in Mälaren, may explain the larger catches of perch there.

Species Interactions

Pikeperch — Pikeperch are primarily pelagic, searching for food off the bottom. Favored habitats are stony reefs at depths of 5–10 m, which have steep slopes to 20 m.

In both lakes, the majority of pikeperch generally migrate westward to shallow areas to spawn. The greatest migrations occur in Mälaren where fish also ascend one of the tributaries (Svärdson 1948; Rundberg 1968). A smaller proportion of pikeperch in Hjälmaren migrate into the western area (Rundberg 1971). Spawning occurs in the tributaries of Mälaren and western Hjälmaren around April and May, respectively, and continues until mid-June in the deeper eastern parts of the lakes.

In Hjälmaren rainbow smelt (*Osmerus mordax*) is the predominant food item for pikeperch up to 50 cm long (Svärdson and Molin 1968). During the 1960s, when the rainbow smelt population was near extinction, pikeperch fed on young Eurasian perch, bleak (*Alburnus alburnus*), and roach. Other lakes without smelt have pikeperch with normal growth but in Hjälmaren they were thin and growth was less than normal in the absence of its preferred food (Svärdson and Molin 1968).

The decrease in population of rainbow smelt during the 1950s was probably due to the very strong 1959 year-class of pikeperch (Svärdson and Molin 1973). During these years pikeperch were found in areas where they had not occurred normally. Since the population of pikeperch is denser in Hjälmaren than in most other lakes, alternative food sources were probably not sufficient for normal growth.

Growth rates for pikeperch in the two lakes are different (Svärdson and Molin 1968, 1973). Earlier spring warming, higher summer temperature, and lower average lake depth contribute to faster growth in Hjälmaren.

Year-class fluctuations of pikeperch in both lakes have been linked to air temperatures (Svärdson and Molin 1973). Strong year-classes have been correlated to summer air temperatures, especially during July and August. Higher correlations were found in Mälaren.

Eurasian perch — Two types of perch are recognized by their behavior and coloration in both lakes. More vividly colored littoral perch are found to depths of 5 m but usually frequent shallower areas and are mainly bottom feeders. The pale variety feed in the pelagic zone and are found to depths of 10 m.

During summer in Mälaren perch concentrate in a thin layer in the pelagic zone. Movement into the pelagic area and then to the surface is observed from catch records of the trap-net fishery for cisco. In Hjälmaren most perch are found on the slopes from the shoal areas down to the central basin at depths of 15–18 m. In early fall they move to depths of 15–20 m in Mälaren and 10–15 m in Hjälmaren. Spawning in both lakes occurs in all shallow areas where water circulation is good.

Pelagic perch feed primarily on rainbow smelt, whereas the diet of the littoral perch is more varied. Bleak is an important food item for larger perch but roach, Eurasian perch, and ruffe (*Gymnocephalus cernua*) are also eaten.

Northern Pike — During the first 2 yr of life northern pike remain inshore all summer. When northern pike abundance is high, a few larger pike become more pelagic and prey on cisco (*Coregonus albula*) and rainbow smelt.

Spawning takes place in flooded areas or in shallow areas near reeds or other dense vegetation. Water level during and after spawning is an important factor determining year-class size (Svärdson 1964). Low water levels in the spring during 1971–76 resulted from lower than average rainfall and may be responsible for recent weak year-classes of pike. Decreased fishing effort because of reduced market demand has caused an increase in the average size and number of large pike. Cannibalism by large pike may therefore be another factor controlling year-class success.

Trends in Harvest and Associated Environmental Changes

In the 18th century the fish species found in Lake Mälaren (Fisher-ström 1785) were the same as today, except for brown trout (*Salmo trutta*), which was previously caught in considerable numbers but today is extinct. Fisher-ström (1785) mentioned that whitefish (*Coregonus* spp.) were the most important species and pikeperch (the most important species today) was hardly mentioned. Pikeperch was ranked sixth in order of abundance in Hjälmaren (Uggla 1786). At the time of Trybom's (1898) survey in the western part of Mälaren the most important species were pikeperch, northern pike, bream, burbot (*Lota lota*), and asp (*Aspius aspius*). Although whitefish were less evident, other studies (Enkvist 1903; Tengström 1903; Johnsson 1905) showed that they were still important in the eastern part of the lake.

The percentages of pikeperch, northern pike, and Eurasian perch in commercial landings have changed greatly since 1914 (Table 2, Fig. 2). The increase of pikeperch seems to be a process that had already started before 1964. Although average landings of northern pike have changed little, the decrease in Mälaren in recent years can be attributed not only to reduced fishing effort but also to flood-control measures which reduced water levels during the northern pike spawning

TABLE 2. Species compositions (percent) of landings (tonnes) from lakes Mälaren and Hjälmaren for various periods from 1914 to 1974.

Period	Pikeperch	Pike	Perch	Burbot	Cisco	Eel	Whitefish	Total landings (t)
			Mälaren					
1914–23								
% of total	30	25	15	14	9	3	4	284
% excl. whitefish & cisco	34	29	17	16	—	4	—	
1966–74								
% of total	38	10	3	4	44	1	—	383
% excl. cisco	68	18	5	7	—	2	—	
			Hjälmaren					
1914–23[a]	30	13	43	9	—	—	5	213
1947–50[b]	41	23	28	5	—	—	3	
1960–65[b]	52	13	27	7	—	—	1	
1966–74[a]	71	12	12	2	—	—	3	220

[a] Catches from entire lake.
[b] Catches from Örebro county (west end of lake).

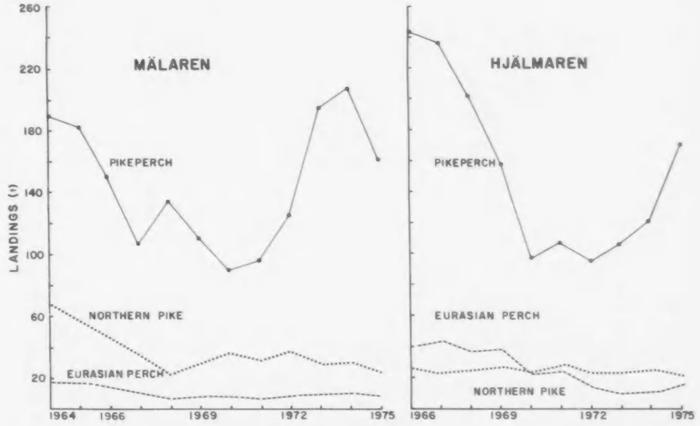

FIG. 2. Commercial landings (tonnes) of three species from lakes Mälaren and Hjälmaren, 1964–75.

period (Ros 1966). Eurasian perch production and relative contribution have also decreased over the years.

Environmental changes known to have occurred in the lakes are eutrophication, the die-off of a huge crayfish population in 1907–08 due to the *Aphanomyces* disease, and flood control. The mortality of crayfish is not known to have affected fish populations. However, older fishermen in Hjälmaren consider that the increase in pikeperch started after the crayfish were killed by *Aphanomyces* sp. Flood control measures in Hjälmaren in the 1880s resulted in a 1.3 m decrease in average water level and a 1.8 m decrease in high water level. Similar control measures in Mälaren since the 1940s have not changed the average water level but have reduced the high water level approximately 0.5 m.

The most likely explanations for the increase of pikeperch in Hjälmaren (Fig. 2) are cultural eutrophication (Svärdson and Molin 1968), the steady increase in organic content and increased turbidity of the water mass because of total circulation (Grimås et al. 1972).

Agricultural activity has always been important around the lakes, and after the draining of

Hjälmaren 18,000 ha of new farmland were created. Increased industrial activity resulted in the rapid growth of cities at the turn of the century. Increased nutrient loads and thus increased turbidity at the time when pikeperch were known to have increased indicate that eutrophication has been favorable for this species.

The sharp decline in Eurasian perch catches in Hjälmaren during 1970–75 (Fig. 2) was more rapid than in earlier years. This decrease can be partly attributed to an increasing unfavorable environment and to increased predation by pikeperch, especially when pikeperch were more abundant during the mid- and late 1960s. The dominant pikeperch population may compete better for food than the sparse population of 1914, since pikeperch and Eurasian perch now have rainbow smelt as common forage.

Since the increasing sports fishery in both lakes concentrates primarily on Eurasian perch, this additional source of stress may be affecting these stocks. Although the total annual angler catch is unknown, large catches are made during all seasons and are estimated to be at least twice the commercial landings. This fishery takes smaller fish than the commercial fishery (Rundberg 1971). Differences in growth rate between 1914 and 1975 (Alm 1917; K. Dahlqvist personal communication), with slightly faster growth in young fish and slower growth at older ages, may be explained by increased fishing pressure on these populations.

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Maintenance of a Walleye, *Stizostedion vitreum vitreum*, Fishery in a Eutrophic Reservoir[1,2]

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Hoover Reservoir, a very eutrophic environment, produces a successful fishery for walleye. However, the population can only be sustained by stocking due to the absence of high quality summer habitat, intensive exploitation, poor recruitment of most natural year-classes, and poor growth of adult walleye. The oxygen temperature regime brought about by eutrophication forces the adult walleye to live at an above optimum temperature regime for maximum growth during the summer months. Because of the climate and geographical location, the preferred temperatures of the desired prey, young gizzard shad, are far above that of the adult walleye. This makes the shad less accessable to predation for a large portion of the day further reducing the growth of older walleye. Poor recruitment of large natural year-classes results from the absence of gizzard shad fry, which spawn much later than walleye, at the time larval walleye convert from a planktonic to a piscivorous feeding habit. Large year-classes of walleye are produced in years when fry were stocked. Stocked fry were produced in hatcheries from spawn obtained at the reservoir. Fry were stocked in the reservoir just at or in advance of shad spawning, whereas in most years naturally produced fry appeared well in advance of shad spawning. This delayed appearance of stocked walleye fry probably accounts for their successful year-class production. This walleye spawning stock had an estimated mean biomass of 13.6 kg/ha and a mean annual production of 2.2 kg/ha between 1967 and 1973.

Key words: Hoover Reservoir — Ohio, Percidae, *Stizostedion*, management, fry stocking

MOMOT, W. T., J. ERICKSON, AND F. STEVENSON. 1977. Maintenance of a walleye, *Stizostedion vitreum vitreum*, fishery in a eutrophic reservoir. J. Fish. Res. Board Can. 34: 1725–1733.

Le réservoir Hoover, un environnement très eutrophe, alimente une bonne pècherie de dorés jaunes. Cependant, la population ne peut se maintenir que grâce à des peuplements, à cause de l'absence d'un habitat estival de haute qualité, d'une exploitation intense, du faible recrutement de la plupart des classes d'âge et de la croissance difficile du doré jaune. Le régime oxygène-température résultant de l'eutrophisation force le doré adulte à vivre à des températures supérieures au régime optimal d'une croissance maximale durant les mois d'été. A cause du climat et de la position géographique, les températures préférées de la proie la plus recherchée, les jeunes aloses à gésier, sont de beaucoup supérieures aux températures préférées du doré jaune adulte. Les proies de ce dernier sont donc moins accessibles durant une bonne partie de la journée, contribuant davantage au ralentissement de la croissance des dorés jaunes plus âgés. Le faible recrutement d'abondantes classes d'âge naturelles résulte de l'absence d'alevins d'alose à gésier, qui fraye beaucoup plus tard que le doré jaune, à une époque où les larves de doré jaune passent d'un régime alimentaire planctonique à un régime piscivore. Les années où il y a peuplements d'alevins produisent de fortes classes d'âge de dorés jaunes. Les alevins en-

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semencés sont produits dans des écloseries à partir de frai obtenu au réservoir. Les peuplements d'alevins dans le réservoir ont été effectués juste au moment, ou un peu avant, où l'alose fraye, alors que la plupart du temps, les alevins produits naturellement apparaissent longtemps avant la fraie de l'alose. Cette apparition tardive d'alevins de doré jaune ensemencés est probablement responsable du succès des classes d'âge. Entre 1967 et 1973, ce stock de dorés jaunes reproducteurs avait une biomasse moyenne estimée de 13.6 kg/ha et une production annuelle moyenne de 2.2 kg/ha.

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DESPITE being very eutrophic, Hoover is the only reservoir that provides an extensive sport fishery for walleye (*Stizostedion vitreum vitreum*) in central Ohio. Even though immature walleye grow very fast, adults have a very reduced growth and high mortality. We decided to investigate the reasons for this as well as to determine if the population was self sustaining in the face of intensive exploitation within a rigorous environment or whether it could only be maintained by a stocking program. Walleye were introduced in 1955 as fry and except for 1960 were stocked annually from 1955 to 1965. Hoover Reservoir is a 1143 ha impoundment located in central Ohio. It was constructed by the City of Columbus as a water supply reservoir in 1954 by the impoundment of two small creeks, Big Walnut and Little Walnut. Table 1 provides a physical description of the reservoir. Walleye, *Stizostedion vitreum vitreum*, is the principal game fish.

In order to evaluate whether the population was self sustaining we stocked no fry in 1966 and 1967 and then stocked fry only in alternate years beginning in 1968. We then followed the contribution of each year-class to the fishery in order to establish if "stocked" year-class made substantially better contributions to the fishery than year-classes that appeared when no stocking took place.

Methods

We used the Schumacher–Eschemeyer mark-and-recapture method from 1966 to 1972 to estimate the population density of the spawning stock. Six to 11 fyke nets were set each spring to collect mature walleye during their spawning period. The nets were from 1.86 to 4.4 m in length with a 11.4-mm stretched mesh. Netting (Fig. 1) was initiated when water temperatures approached 5°C and continued at least until spawning had ceased.

Fry produced in hatcheries from spawn collected in the reservoir were stocked. These fry were released into the reservoir between April 24 and May 1.

The biomass for a given year was determined by multiplying the estimated number of each age-group by the mean weight per fish and summing the contributions from all age-groups.

Where the data permitted us to do so, we calculated the annual production of the spawning stock. The data are limited in that we used a growth rate averaged over several years to determine *G*, the instantaneous rate of growth. Also, for certain age-groups the survival rate was assumed to be 100%;

TABLE 1. Physicochemical characteristics of Hoover Reservoir (After Birch 1969).

Total length (km)	13.7
Maximum width (km)	2.4
Maximum depth, lowest basin (m)	21.0
Mean depth, all basins (m)	6.5
Surface area (hectares)	1143.3
Drainage basin (km)	492.1
Maximum volume (10^6 m^3)	74.4
Shoreline length, all basins (km)	72.4
Shoreline development factors, all basins	11.98
Growing season (days surface temperature >5.5°C)	242
Morphoedaphic index (Ryder 1965)	30.6
Total dissolved solids (x ± SD) mg/ℓ	199.4±8.6

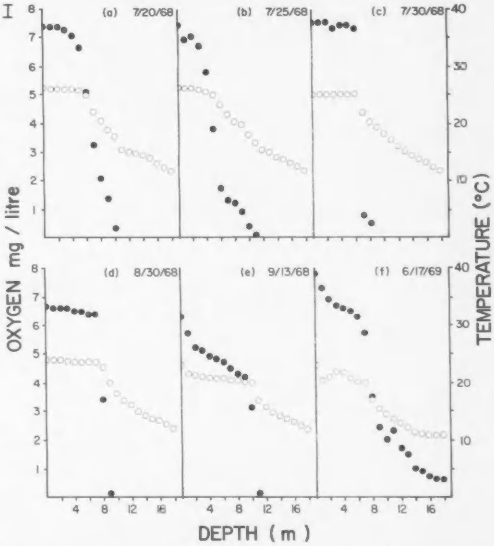

FIG. 1. Hoover Reservoir, showing depth contours (m) and locations of trap nets during spring trapping.

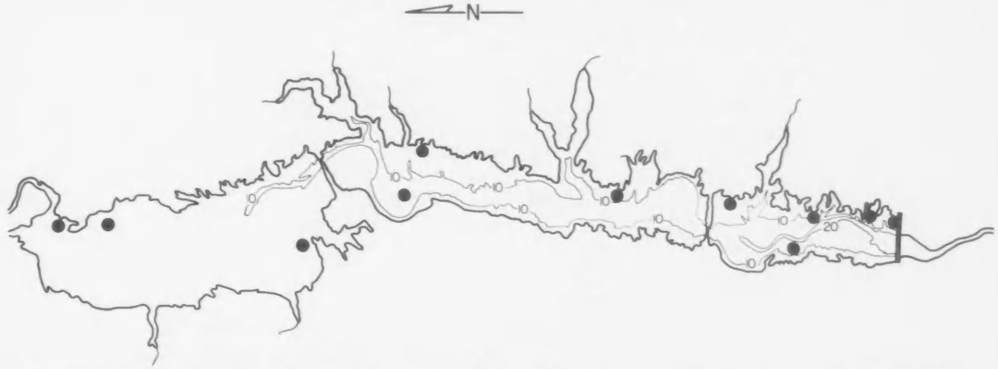

FIG. 2. Typical temperature and dissolved oxygen regimes during the summer in the deepest basin of Hoover Reservoir. White dots give temperature, black dots oxygen in mg/ℓ.

the relevant production values represent overestimates. Only in 1972–73 did the treatment of such data alter the estimate by a large amount.

Age composition was determined from scale samples (Tucker and Taub 1970; Erickson 1973). Fish were tagged with sequentially numbered Floy dart tags in 1966–67 and Floy anchor tags in 1968–73.

Angler harvest was determined by the stratified creel census for the years 1968–73. A total of eight surveys were conducted each month, four on weekdays and four on weekend days. The creel checks ran from 0800 to 1200 h and from 1600 to 2000 h.

Physical and Chemical Characteristics of Hoover Reservoir

The reservoir is divided into three basins by two causeways (Fig. 1). The northern basin is the widest and shallowest, with much of the area less than 4 m deep. The middle and lower basins are not as wide and are much deeper.

The soil in the area is of Wisconsin glacial outwash gravel overlain with 1–3 m of moderately calcareous clay loam till. Shale banks are present on the west shore of the middle basin and along the east shore adjacent to the dam.

The annual water level fluctuates 3–6 m. As water levels slowly recede wave action produces clean gravel bars which can be used by spawning walleyes.

The reservoir is a very eutrophic environment. The reservoir is in a predominantly agricultural area that is slowly becoming urbanized. As a result the watershed supplies large amounts of nitrate (352,374.6 kg/yr) and phosphate (144,013.9 kg/yr) annually to the reservoir (Birch 1969). Of the total nutrients entering the reservoir as total phosphate, 41.3% comes from agricultural runoff, 28.2% from reservoir sediments, 26.3% from wastewater effluent and the remainder from urban runoff, ground water, and direct precipitation into the reservoir (Birch 1969).

In addition, large quantities of ammonia are stored in the sediments. As fall overturn proceeds, nitrification of this ammonia results in large increases in nitrate in the winter months (Birch 1969). The lower basins become stratified during the summer with respect to several chemical characteristics. Anoxic conditions in the deeper portions of the reservoir persist for nearly 4 mo during the summer and fall in the middle and lower basins. Typical summer stratification is shown in Fig. 2.

Characteristics of Fish Populations

In 1954, when the dam was closed, the reservoir was stocked with fingerling largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), crappie (*Pomoxis* sp.), bullhead (*Ictalurus* sp.), channel catfish (*Ictalurus punctatus*), and muskellunge (*Esox masquinongy*), and walleye fry. In 1954 carp (*Cyprinus carpio*) and gar (*Lepisosteus* sp.) were removed by trap in order to reduce populations of these species. In 1967–68 adult white bass (*Morone chrysops*) were introduced (Erickson 1973).

Annual sampling with fyke nets from 1954 to 1973 showed three patterns of predominance. White crappie were the predominant game species from 1954 to 1959, walleye and brown bullheads during 1960–66 and white bass from 1967 to the present (Table 2). Altogether, 29 species of fish are known from the reservoir (Tucker 1968).

Seine and trawling operations show that young-of-the-year gizzard shad (*Dorosma cepedianum*), white crappie (*Pomoxis annularis*), and yellow perch (*Perca flavescens*) are the predominant forage species for walleye in the reser-

TABLE 2. Average percentages of total captures by fyke nets from Hoover Reservoir represented by various game and adult forage fish during three periods, 1954–73[a].

Species	1954–59	1960–66	1967–73
Game and food fishes			
Pomoxis annularis	23.7	12.6	15.9
Lepomis macrochirus	20.9	3.0	5.3
Pomoxis nigromaculatus	10.0	6.1	5.6
Stizostedion vitreum	.7	14.8	17.9
Morone chrysops			18.1
Ictalurus nebulosus	4.8	19.6	10.0
Ictalurus punctatus	.6	5.5	2.3
Micropterus salmoides	.8	2.1	.6
Miscellaneous	1.7	.2	.4
Total	63.2	63.9	76.1
Adult forage fishes			
Moxostoma sp.	13.3	6.5	1.8
Mynetrema melanops	1.4	11.6	6.8
Cyprinus carpio	7.4	5.2	2.1
Dorosoma cepedianum	5.8	1.2	4.7
Carpiodes cyprinus	1.2	8.2	7.3
Catostomus commersoni	6.8	3.0	.6
Miscellaneous	.9	.4	.6
Total	36.8	36.1	23.9

[a] Six to eleven fyke nets 1.86–4.4 m in length with an 11.4 mm. stretch mesh were set at the locations indicated by the black dots on Fig. 1 during the spawning period in each year.

voir in order of abundance (Tucker 1968). Although suckers and carp are fairly abundant as large adults (Table 2), few are taken in trawls or seines as young-of-the-year. This is probably because of fyke net selectivity for these forage fish.

Population Size and Age Composition

Schumacher–Eschemeyer estimates show that the spawning population varied about fourfold during the period of investigation.

Year	Estimate ± 95% confidence limits
1967	42,489 ± 4,648
1968	16,639 ± 2,638
1969	10,627 ± 2,466
1970	12,761 ± 1,550
1971	20,286 ± 4,694
1972	16,759 ± 4,430
1973	25,064 ± 6,376

Recruitment to the spawning stock occurs at age 2. The spawning stock is mainly composed of sexually mature males 2-yr-old and older and mature females 3-yr-old and older (Table 3).

The large 1967 population was composed of 3- and 4-yr-old males from the strong 1964 and 1965 year-classes (Table 3). By 1969 the population drastically declined as a result of almost total recruitment failure of the 1967 year-class and poor survival to age 3 of the moderately sized 1965 year-class. In 1970 the spawning population increased due to recruitment of the 1968 year-class (Table 3). In 1971 the population further increased due to recruitment of the 1969 year-class. This was the only large year-class which appeared when no fry stocking took place. In 1972 the population declined despite recruitment of 9,802 males from the 1970 year-class. This decrease resulted from the sharp decline in the 1969 year-class from 12,200 fish in 1971 to 3,379 in 1972 (Table 3). In addition the 1970 year-class was grossly underestimated in 1972. Perhaps this large year-class grew too slowly to be fully recruited by the fyke nets at age 3. An estimate of the 1970 year-class was much higher in 1973. The large increase in the spawning population in 1973 was the result of the large recruitment of this 1970 year-class.

Growth Rate

Older walleye in Hoover Reservoir show a poor growth response despite their low density in the population. The lack of a growth response of older fish may be the result of three factors: the absence of good quality summer habitat forcing them to live at their upper metabolic range, poor

TABLE 3. Numbers of male and female spawning walleyes of various ages in Hoover Reservoir, 1967–73[a]. Year-classes produced when fish were stocked are underlined.

Age	Sex	1967	1968	1969	1970	1971	1972	1973
1	M	—	—	—	21	69	88	—
	F	—	—	—	72	—	—	—
2	M	258	7720	1053	7778	12200	9802	3638
	F	—	446	—	437	—	10	958
3	M	16287	4429	1806	407	4577	2765	15357
	F	3143	1779	293	458	556	914	3365
4	M	11523	1206	3805	511	331	1243	382
	F	1327	708	3155	378	1844	655	347
5	M	6094	525	—	1543	296	468	583
	F	548	106	515	773	104	202	104
6	M	2400	—	—	167	122	234	101
	F	167	—	—	138	60	170	79
7	M	258	—	—	—	17	15	40
	F	145	—	—	65	207	85	30
8	M	111	—	—	—	—	—	—
	F	23	—	—	37	109	42	60
9	M	—	—	—	—	—	—	—
	F	11	—	—	—	—	—	—

[a] The totals in Table 4 do not coincide with the total estimates in the text. Except in 1969 and 1973, some immature fish were included in the mark-and-recapture totals but not in the age frequency distributions used to calculate the age compositions in Table 4.

TABLE 4. Average lengths (mm) of Hoover Reservoir male and female walleye of various ages for 1967–73. Data for 1967–68 from Tucker and Taub (1970); for 1969–73, from Erickson (1973). Fish were collected in April of each year.

	1967–68		1969–73	
Age	Males	Females	Males	Females
1	254(269)[a]	259(258)	215(416)	216(267)
2	369(268)	372(258)	373(461)	384(267)
3	424(156)	429(151)	436(301)	444(251)
4	451(73)	460(83)	478(96)	527(97)
5	464(29)	489(41)	497(53)	558(64)
6	487(5)	497(18)	525(15)	589(35)
7	502(3)	508(9)	541(4)	620(14)
8	—	515(3)	—	663(6)
9	—	535(2)	—	740(1)
10	—	570(1)	—	—

[a] Number in parenthesis is sample size.

utilization of the available forage due to its lack of availability for a large portion of the day, and the metabolic stress encountered by these older fish during their foraging activity.

Because of slight differences between the two periods 1967–68 and 1969–73 fish growth rates are presented separately for the purpose of calculating biomass and production. The pattern of growth increments in this population is rather striking (Table 4). Both in 1967–68 and 1969–73, following a rapid increase in length and weight during the first and second year, growth increments drastically decrease (Table 4 and 5). As a result of poor survival of most year-classes after age 2 or 3, very few older fish (4+) remain in the population. Despite their low density, the growth rate of these older fish is very poor.

Hoover Reservoir, during summer months, provides poor quality summer habitat for adult walleyes. Adequately oxygenated water (5 mg/ℓ) occurs only at high temperatures sometimes as high as 25°C (Fig. 2). Walleyes exhibit a strong aversion to water temperatures of 24°C (R. B. Fitz and J. A. Holbrook, T.V.A., unpublished

TABLE 5. Mean empirical weights (g) of walleye of various ages in Hoover Reservoir for 1967–68 and 1969–73. Data for 1967–68 from Tucker and Taub (1970); for 1969–73, from Erickson (1973). Fish were collected in April of each year.

	1967–68		1969–70	
Age	Males	Females	Males	Females
1	312	312	312	312
2	452	510	482	510
3	652	680	709	737
4	794	879	964	1361
5	935	1133	1049	1757
6	1077	1190	1361	1871
7	1247	1275	1475	1928
8	—	1304	—	2211
9	—	1417	—	3345
10	—	2211	—	—

data) showing a preference for water at 20°C (Bennett 1971).

Besides living at suboptimal water temperatures older walleye do not have full access to their principal forage, the young gizzard shad (*Dorosoma cepedianum*). The shad are located during the summer at water temperatures far above the preferred temperatures of the mature walleye. Gizzard shad are a predominantly littoral species and in the summer are found in the warmest water available to them (Jester and Jensen 1972). The preference of gizzard shad for warm water makes them unavailable to large adult walleye for a large part of the day. Stroud (1949) found that walleye feed heavily on gizzard shad up to 75 mm. Trawl catches and shore seining show that gizzard shad of a size suitable for adult walleye are found in the warm shallow littoral zone (Tucker 1968). For example, from July 31 to August 31, gizzard shad 59 mm in mean length (R: 43–93) make up 79% of the catch during shore seining.

Walleye do move at dusk into shallow warm water to feed on the gizzard shad. This periodic movement at dusk from cooler water into warm water further affects their growth performance by reducing their food conversion efficiency. The maintenance requirements of walleyes are very high at 20°C (Kelso 1972) and probably much higher at 25°C, the temperature at which they often forage on the gizzard shad. These high maintenance requirements are further increased by the feeding movement at dusk of the adults from poorly oxygenated cool water to the warmer waters. Fish undergoing cyclic changes in water temperatures have a lower food conversion efficiency than fish maintained at constant temperatures (Kelso 1972). Thus these walleyes during summer not only live at the upper metabolic range for their maintenance requirements but the cyclic changes in their temperature regime further stresses their ability to efficiently utilize their forage.

Adult gizzard shad are present in deeper water but cannot be utilized. Walleyes less than 50.8 cm in total length do not forage on adult shad (Stroud 1949). The vast majority of walleye in Hoover Reservoir are less than 45 cm in length (Table 4). We feel that a combination of the above factors suppresses the growth rate of adult walleye.

Biomass and Annual Production

The estimated mean biomass of the spawning stock of walleye in Hoover Reservoir for the period 1967–1973 was 13.57 kg/ha and ranged from a high of 28.88 in 1967 to a low of 8.13 in 1970 (Table 6). In general annual production of the mature fish was very low on a kg/ha basis. As expected the youngest age-groups contributed most of the production. Values ranged from a low of 1.31 kg/ha in 1969–70 to 4.05 in 1972–73 (Table 7). The mean value was 2.16 kg/ha. In general the productivity of the reservoir for walleye seemed to be increasing with time. Later year-classes had a higher production than year classes hatched in earlier years 1965–67. Year-classes tended to have higher production in those years when fry were stocked. More data is needed to verify this tendency.

Mortality and Angler Harvest

Intensive angling on age 2 and 3 fish truncates the age structure of the population (Table 3). Except for 1967–68, anglers accounted for 40 to 81% of the total mortality of age 3+ fish and 30–50% of the total mortality of the entire stock (Table 8).

In this very eutrophic environment, the intensive exploitation by anglers of the walleye can only be sustained through supplemental reinforcement of natural year-class production by fry stocking. Angler harvest begins in mid-April and reaches a peak in late May. Only when a large year-class is recruited (1969 and 1971) does a significant harvest of fish under 330 mm occur. The total harvest of walleyes including number of walleye under 330 mm and young-of-the-year 1968–1973 were as follows:

Year	Total	Under 330 mm	Young-of-the-year
1968	5385	499	22
1969	2337	1221	198
1970	3481	302	79
1971	11620	6513	245
1972	4364	303	—
1973	1126	171	—

TABLE 6. Biomass (kg) estimates of spawning stocks of male and female walleye in Hoover Reservoir, 1967-73 in kg/ha.

	1967		1968		1969		1970		1971		1972		1973	
Age	M	F	M	F	M	F	M	F	M	F	M	F	M	F
1							6.6	22.5			27.5			
2	116.6		3493.5	227.5	507.5		3749.0	222.9	21.5		7665.2	5.1	1743.5	488.6
3	10619.1	2137.2	2886.4	1209.7	1280.5	216.0	288.6	337.5	5880.4	409.8	1960.4	673.6	10888.1	2480.0
4	9149.3	1166.4	957.6	622.3	3688.0	4294.0	492.6	514.5	3245.1	2509.7	1198.3	891.5	368.2	472.3
5	5697.9	620.9	490.9	120.1		904.9	1618.6	1358.2	319.1	182.7	490.9	354.9	611.6	182.7
6	2584.8	198.7					227.3	258.2	310.5	112.3	318.5	318.1	137.5	147.8
7	321.7	184.9						125.3	166.0	399.1	22.1	163.9	59.0	57.8
8	154.2	28.7						81.8	25.1	241.0		92.9		132.7
9		15.6												33.4
Total kg	28643.6	4376.6	7828.4	2179.6	5476.0	5414.9	6382.7	2920.9	9967.7	3854.6	11655.4	2500.0	13817.9	3995.3
Total kg/ha	25.05	3.83	6.85	1.91	4.79	4.74	5.58	2.55	8.72	3.37	10.19	2.19	12.09	3.49
Total M&F kg/ha	28.88		8.76		9.53		8.13		12.09		12.38		15.58	

TABLE 7. Production (kg) of various age-groups and of associated year-classes of walleye in Hoover Reservoir, 1967–73. Note that values in parentheses are estimates based on assumption that the value of Z was equal to 0 (see text).

	1967–68		1968–69		1969–70		1970–71		1971–72		1972–73	
Age group	M	F	M	F	M	F	M	F	M	F	M	F
					Annual production							
2–3	(52.2)		787.2	70.1	152.2	(181.6)	1371.0	99.8	1402.4	(344.5)	(3656.1)	345.1
3–4	804.7	319.7	591.7	(359.2)	255.2	671.5	94.1	283.7	635.9	288.0	296.5	116.9
4–5	485.3	114.4		151.0	202.2	31.0	31.4	84.2	(26.6)	(11.3)	69.9	14.2
5–6							166.2	30.2	81.9	(3.4)	72.8	4.6
							7.3	7.9	5.7	(59.9	12.3	20.8
								12.3				23.9
Total	1342.2	434.1	1378.9	580.3	609.6	884.1	1670.0	518.1	2152.9	707.1	4107.6	525.5
Total M&F	1776.1		1959.2		1493.7		2188.1		2860.0		4633.1	
Total (kg/ha)	1.55		1.71		1.31		1.91		2.50		4.05	
					Year-class production beginning at age 2							
Year-class	65[a]		66		67		68[a]		69		70[a]	
Production	1311.1		1989.7		936.9		2477.8		2160.3		4001.2	

[a] Fry stocked.

TABLE 8. Estimates of the distribution of loss for age 3+ fish between angling catch and natural mortality.

Year	Total mortality (Table 4)	Angler harvest	Natural mortality	Percentage of total mortality due to fishing
		Age 3+ fish		
1967–68	34,497	4,864	29,633	0.14
1968–69	1,538	918	620	0.60
1969–70	6,352	3,100	3,252	0.49
1970–71	3,231	4,862[a]	—	—
1971–72	5,035	4,061	974	0.81
		Entire spawning stock		
1967–68	34,497	5,385[b]		0.16
1968–69	7,614	2,337		0.31
1969–70	6,998	3,481		0.50
1970–71	6,432	11,620[a]		—
1971–72	14,470	4,364		0.30

[a]Greater than estimated total mortality. Angler harvest of 3+ fish determined by subtracting age I and II fish from total harvest in Table 10.

[b]Values in this column from Table 9.

TABLE 9. Numbers of spawners produced at age 2+ by each year-class during its life spawn compared to number of fry stocked in Hoover Reservoir from 1963 to 1973.

Year stocked	Number walleye fry stocked[c]	Numbers of spawners	Relative ranking[a]
1963	2,000,000	13,481[b]	Excellent
1964	500,000	21,979[b]	Excellent
1965	2,000,000	16,084	Good
1966	0	12,037	Fair
1967	0	2,943	Poor
1968	1,000,000	15,933	Good
1969	0	16,608	Good
1970	1,765,000	28,534	Excellent
1971	0	4,596	Poor
1972	1,000,000		
1973	0		

[a]The mean number of spawners produced was 14,493. We ranked each year-class in relation to the mean.

[b]The 1965 year-class was the first one for which we had totals of fish from age 2+ on. The estimate for the 1963 year-class is for only age 4 and 5 fish; for 1964, only age 3 and 4 fish. The large numbers for these older age-groups indicate that these were very large year-classes.

[c]Fish were stocked between April 24 and May 1.

Except for 1969, good to excellent year-classes were recruited to both the spawning population and the fishery only in those years when stocking of fry occurred (1965, 1968, 1970) (Table 9). Some natural reproduction occurs each year in Hoover Reservoir. However, three of the four natural year-classes (1966, 1967, 1971) produced when no walleye were stocked varied from poor to below average (Table 9). Only the 1969 year-class was at the mean for the period 1964–1973 (Table 9).

Discussion

We believe the production of large year-classes in those years when fry were stocked as well as the appearance of a large natural year-class in 1969 is related to the biology of the principal forage, gizzard shad. In years when stocking takes place the walleye fry used for stocking are hatched from spawn collected in the reservoir in late March and early April when the walleye are gathered on the spawning areas. In most years the reservoir warms rapidly and naturally produced eggs hatch much earlier than eggs taken back to the hatchery. In the hatchery water temperatures are relatively constant. The walleye in the hatchery reach the swim up stage in late April or early May whereas walleye fry in the reservoir reach the swim up stage by mid-April. Zooplankton are very abundant in Hoover (Gartman 1969) and not a limiting food supply for walleye fry. However the lack of forage fish at the time that walleye convert from plankton to fish as a food source could limit the production of a strong year-class. If the fry grow rapidly on the abundant zooplankton they could reach the conversion point in advance of the appearance of forage fish fry and thus starve or cannibalize.

The principal forage are the gizzard shad. Shad spawn in Ohio at a temperature range of 17.8–18.6°C (Jester 1972). Usually when the fry are stocked in late April or early May they enter the reservoir after the shad have spawned.

Naturally produced fry usually appear by mid-April before the Shad spawn. However in 1969, surface water temperatures were quite warm in early May (20°C on May 7, 1969). This allowed the gizzard shad to spawn early and so provide forage for the swim up fry. In 1967, a typical year, a poor natural year-class was produced when May water temperatures were below the temperature at which shad spawn and hatch (16.9°C on May 3, 1967). Jester (1972) showed that strong year-classes also developed in Elephant Butte Reservoir in those years where walleye were stocked after gizzard shad spawned and provided forage. Thus in Hoover the appearance of successful walleye natural year-classes probably coincide with a rapid warming period allowing early gizzard shad spawning. The success of stocked year-classes may in turn depend on their being placed in the reservoir after the shad spawn.

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Changes in Fish Community of Klíčava Reservoir with Particular Reference to Eurasian Perch (*Perca fluviatilis*), 1957–72[1]

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HOLČÍK, J. 1977. Changes in fish community of Klíčava Reservoir with particular reference to Eurasian perch (*Perca fluviatilis*), 1957–72. J. Fish. Res. Board Can. 34: 1734–1747.

Soon after the 1955 filling of the 60 ha mesotrophic Klíčava Reservoir in Czechoslovakia, the fish fauna started to change. Generally, lithophils were replaced by phytophils and then by ecologically more plastic species. Fish biomass increased in the first 12 yr from 65 to 236 kg/ha, but after 1967 dropped to about 170 kg/ha. Increased biomass and density of piscivores were responsible for the decline. Among the piscivores the most important role was played by the pikeperch (*Stizostedion lucioperca*) rather than the Eurasian perch (*Perca fluviatilis*) or northern pike (*Esox lucius*). Cyclical changes in the age structure of the perch population and the periodical occurrence of many young resulted from fluctuations in the rate of cannibalism, which affected the density of the fry and yearlings. A decline in zooplankton biomass and disappearance of larger zooplankters in the first 5–6 yr of the reservoir were due to increased density of fish, especially perch, which fed on zooplankton. Synchronous predation by piscivores and zooplanktivores produced a nearly stable zooplankton biomass in the later years of the reservoir. The perch is a highly specialized species which behaves in the fish community more or less autonomously, because it is able to control its own density in accord with its food resources. The above conclusions are based on a literature review and analyses of new data.

Key words: Percidae, community ecology, *Perca*, biomass, density, production, predation

HOLČÍK, J. 1977. Changes in fish community of Klíčava Reservoir with particular reference to Eurasian perch (*Perca fluviatilis*), 1957–72. J. Fish. Res. Board Can. 34: 1734–1747.

Peu après le remplissage en 1955 du réservoir Klíčava mésotrophe de 60 ha en Tchécoslovaquie, la faune ichtyologique commença à changer. En général, les lithophiles furent remplacés par les phytophiles et ensuite par des espèces écologiquement plus plastiques. La biomasse des poissons augmenta durant les 12 premières années de 65 à 236 kg/ha, mais après 1967 tomba à 170 kg/ha. L'augmentation de la biomasse et de la densité des piscivores a été responsable du déclin. Parmi les piscivores, le sandre, *Stizostedion lucioperca*, joua un rôle plus important que la perche eurasienne, *Perca fluviatilis*, ou le grand brochet, *Esox lucius*. Les changements cycliques de la structure en âge de la population de perches et l'occurrence périodique d'un grand nombre de jeunes résultèrent de fluctuations du taux de cannibalisme, affectant la densité des alevins et des jeunes de l'année. Un déclin de la biomasse du zooplancton et la disparition des grands zooplanctontes durant les 5–6 premières années du réservoir ont résulté d'un accroissement de densité des poissons, surtout de la perche, qui se nourrit de zooplancton. La prédation synchrone par les piscivores et les zooplanctivores produisit une biomasse de zooplancton presque stable durant les années subséquentes du réservoir. La perche est une espèce hautement spécialisée qui se comporte de façon plus ou moins autonome dans la communauté de poissons, car elle est capable de contrôler sa propre densité selon les ressources alimentaires disponibles. Les conclusions qui précèdent sont fondées sur une revue de la littérature et l'analyse de nouvelles données.

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LAKE Klíčava is a reservoir which has been investigated by hydrobiologists and ichthyologists almost from its first filling. Because fish stocks were quantitatively studied with the same methods throughout these years, both the gradual development of populations of particular species and some causal relations can be analyzed. The purpose of my paper is to describe changes from 1957 to 1972 in fish stocks and to analyze some causal relationships in a community that received almost no fishing pressure. Data are from the

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TABLE 1. Areas, volumes, maximum and mean depths, total dissolved solids (TDS), and morphoedaphic indexes (MEI) of the Klíčava Reservoir 2 yr after filling (1957) and later (1964, 1967–72). (Source — see acknowledgments.)

Year	Area (ha)	Volume (10^6 m^3)	Depth (m) maximum	Depth (m) mean	TDS (mg/ℓ)	MEI (TDS ÷ mean depth)
1957	60.7	8.16	35.0	13.4	—	—
1964	54.0	6.71	33.1	12.4	237	19.1
1967	60.9	8.20	35.0	13.5	241	17.9
1968	60.4	8.11	34.8	13.4	228	17.0
1969	60.0	8.03	34.2	13.4	243	18.1
1970	60.3	8.09	34.4	13.4	279	20.8
1971	58.6	7.76	34.0	13.2	321	24.3
1972	52.4	6.36	30.7	12.1	398	32.9
Mean	58.4	7.68	33.9	13.1	278	21.4

literature and the data files at the Hydrobiological Laboratory in Prague and at the Klíčava Water Works. The analyses here are primarily new but are also from a historical review of published material. Special attention is paid to Eurasian perch, the most important fish in the reservoir and one of two percids occurring there. The effects of increased populations of predators and cannibalism, as well as changes in the limnology of the reservoir, are analyzed.

Description of the Reservoir

Physics, chemistry, and geology — Klíčava, in central Bohemia, is approximately at 50°5′N and 13°55′E and at an altitude of 296 m. It was built during 1949–55 to supply drinking water and for flood control. Surface area averaged 58 ha and fluctuated between 52 and 61 ha from 1957 through 1972 (Table 1). These fluctuations were accompanied by corresponding variations in mean and maximum depths, volume, total dissolved solids, and morphoedaphic indexes. Averages were maximum depth 34 m, mean depth 13 m, volume $7.7 \times 10^6 m^3$, TDS 278, and MEI 21. The shoreline of this elongate, V-shaped lake, including an island, is about 13 km. The longer arm is the flooded valley of Klíčava Brook; the shorter, that of the Lánský Brook. The inlets supply 180 ℓ/s and water is drawn from screened intakes for water supply. Screening prevents migration of fish except during heavy floods. The banks are mostly artificial, very steep, and covered with riprap and stones. The only extensive shallows are at the two inlets; 13 ha are shallower than 5 m and 24 ha shallower than 10 m. The flushing rate is 0.3–2.7 yr. Before filling, all trees were cut near the ground, shrubs were burned, the grass was cut, the meadows were ploughed and rolled, and all debris of plants was cleared away.

The drainage area is 79.9 km², of which 70% is covered by mixed forests and 30% is agricultural. According to Čepek (1936) this region is formed mainly by Algonkian slates as well as by igneous rocks. Human population in the watershed is about 1180. Klíčava Brook originates 17.9 km above the dam and flows through several ponds. Lánský Brook is short and flows mainly through forest of the Lánsky Enclosure. Except for bituminous shale mining since the late 1960s, there is no industry, and the public is excluded both from the enclosure and the reservoir.

Annual rainfall ranges between 30 and 70 cm, annual air temperature averaged 8.0°C from 1901 to 1950, and the growing season averaged 193 days from 1970 to 1972.

Based on the values for transparency, alkalinity, nitrogen, and phosphorus, the reservoir can be classified as mesotrophic. Chemical and physical data from 1961 to 1971 (Table 2) were supplied by the Hydrobiological Laboratory of Czechoslovakia Academy of Sciences in Prague.

Total N (0.6 mg/ℓ) and NO_3-N(0.3 mg/ℓ) were stable from 1959 to 1964 but increased gradually in subsequent years (Fig. 1). The sum of organic and ammonia nitrogen (Naos) in the water fluctuated; it was shown to be related to retention time during the first years of the reservoir (Brandl 1974). Total phosphorus decreased continuously from 1955 to 1972 (Fig. 1). According to Procházková (1975) the increased nitrogen was correlated with increased use of fertilizers in agriculture. Increasing alkalinity resulted from pumping water from bituminous shale mines (M. Straškraba personal communication).

Mean summer temperature of the trophogenic layer is about 20°C, and maximum temperatures fluctuate near 24°C. Ice cover averages 83 days, and the thickness varies between 20 and 30 cm. Hypolimnetic oxygen in late summer is near zero, and in the early years of the reservoir Rozmajzlová-Reháčková (1966) observed 1.0 mg/ℓ or less at 6 m below the surface in August and September. Initially, the color of the water was yellow, then changed to greenish yellow, to green, depending on the density and species composition of phytoplankton.

Biology — No algal bloom has been observed. The total number of phytoplankters increased from 33,700 colonies and cells per litre in 1955 to 2,101,000 in 1959 (Rozmajzlová-Reháčková 1966). Biomass (B. Desortová personal communication) from 1961 to 1969 averaged 1.66 mg/ℓ over the year but

TABLE 2. Mean chemical and physical data (mg/ℓ except as indicated) for Klíčava Reservoir, 1961–72. (Source — see acknowledgments.)

Characteristic	Mean Annual	 April–Sept.
Total N	1.04	1.13
Naos[a]	0.40	0.43
NH_4-N	0.045	0.038
NO_3-N	0.55	0.60
NO_2-N	0.007	0.008
O_2	10.22	10.66
Ca	46.5	45.3
Mg[b]	21.3	20.6
Na[c]	10.3	9.5
K[c]	4.5	4.3
Cl[d]	19.9	10.7
PO_4-P (µg/ℓ)	4.1	2.4
Total P (µg/ℓ)	15.9	15.4
B.O.D. (20°C)	1.72	1.90
C.O.D. (20°C)	12.4	13.3
Alkalinity (mval/ℓ)	1.77	1.66
Hardness (mval/ℓ)	3.2	3.1
Conductivity (10^{-6} ohm^{-1} cm^{-1} at 25°C)	335	346
TDS (derived from conductivity)	266	260
Secchi disc (m)	3.9	3.4
pH	7.8	8.2
Temperature (°C)	12.4	17.0
Color (Hazen units)	11	12

[a] Sum of organic and ammonia nitrogen dissolved in water and seston.
[b] 1970–72.
[c] 1970.
[d] 1970, 1972.

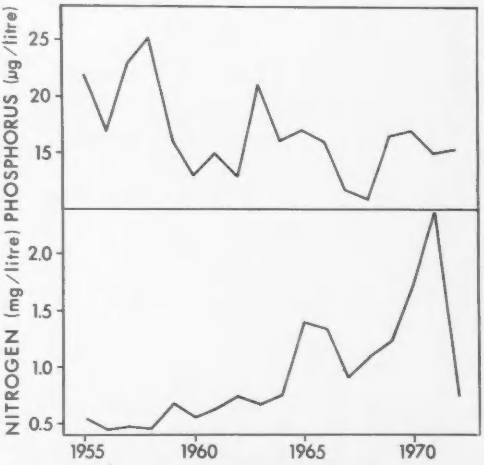

FIG. 1. Changes in total phosphorus and total nitrogen from 1955 to 1972 in Klíčava Reservoir (April to September means).

2.64 mg/ℓ in summer. Gross primary production averaged 1.51 mg·m^{-2}·day^{-1} over the year, but 2.31 in summer.

One hundred and ninety species of phytoplankton have been reported for the Klíčava (Rozmajzlová-Řeháčková 1966). Typical genera initially were *Dinobryon*, *Fragilaria*, *Asterionella*, *Ceratium*, *Cryptomonas*, *Trachelomonas*, *Planktosphaeria*, and *Staurastrum*, but the phytoplankters in 1971–73 (B. Desortová personal communication) were the flagellates *Rhodomonas lacustris*, *Crytomonas curvata*, *C. reflexa*, *Trachelomonas volvocina*, *Peridinium willei*, *P. cinctum*, and *Ceratium hirundinella*, the diatoms *Cyclotella comta*, *Stephanodiscus hanzschii*, *Asterionella formosa*, and *Fragilaria crotonensis*, and the green algae *Scenedesmus bijuga*, *S. arcuatus*, *S. brasiliensis*, *Oocystis parva*, *Crucigenia tetrapedia*, *Tetraodon minimum*, *Phaocottus lenticularis*, *Pandorina morum*, *Coelastrum microporum*, *Nephrocyctis agardhium*, *Ankyra ancora*, and *Chodatella ciliata*.

Of the 68 species of zooplankton, the most common genera were the rotifers *Kellicotia*, *Polyarthra*, and *Keratella* spp., the cladocerans *Daphnia*, *Ceriodaphnia*, and *Bosmina* spp., and the copepod *Eudiaptomus* sp. Though nannozooplankton regularly increased from 13,500/ℓ in 1955 to 28,700/ℓ in 1959, the net zooplankton decreased slightly. Zooplankton biomass expressed in nitrogen content decreased from about 0.6 g/m² in 1956 to about 0.2 g/m² in 1961. From then to 1970 it varied little (see Table 6). Since the numbers of zooplankton did not decline remarkably from 1955 to 1959, both Rozmajzlová-Řeháčková (1966) and Brandl (1974) consider that selective feeding by the increasing number of fish cropped the larger zooplankton, as was postulated by Hrbáček (1962).

Management — With the exception of occasional angling by a few persons with admission to the reservoir, fishing in the reservoir is forbidden. Water quality deteriorated beginning in 1959 as cladocerans decreased in abundance. This suggested that the increased perch population had been responsible, owing to its predation on large cladocerans. Thus, three measures were taken to control the perch density. During 1959–63 about 6000 yearling and 2-yr-old brown trout (*Salmo trutta fario*) and 101 3-yr-old huchens (*Hucho hucho*) were introduced. From 1965 to 1972 about 30,000 yearling pikeperch were also introduced. To limit the number of yearling perch and roach (*Rutilus rutilus*), the water level was reduced in 1957 by 1.2 m, in 1965 by 0.5 m, in 1967 by 0.25 m, in 1969 by 0.3 m, and in 1970 by 0.5 m. The lowering was just after the maximum spawning of perch in 1957 and after that of roach in all other years. From 1964 to 1972 the Forestry Administration fished for perch and roach with traps and gill nets and annually removed about 1000 adult perch and roach. However, except for increasing the number of predators, almost none of these activities had

TABLE 3. Lampreys and fishes found in the Klíčava Brook prior to damming and in three later periods (Oliva 1949; Holčík 1970; O. Oliva and K. Pivnička personal communication). (—Present, ----- Probably present.)

Family— Species	Klíčava Brook 1949	Klíčava Reservoir		
		1956–57	1962–64	1967–75
Petromyzonidae				
Lampetra planeri	—			
Salmonidae				
Salmo trutta m. fario	—	—		
Salmo trutta m. lacustris		—	—	—
Salmo gairdnerii (introduced 1975)				—
Hucho hucho (introduced 1960)			—	
Esocidae				
Esox lucius		—	—	—
Cyprinidae				
Rutilus rutilus		—	—	—
Leuciscus cephalus		—	—	—
Phoxinus phoxinus	—	—	—	
Scardinius erythrophthalmus			—	—
Tinca tinca		—	—	—
Gobio gobio			—	—
Abramis bjoerkna			—	- - -
Abramis brama			—	—
Carassius carassius			- - -	—
Cyprinus carpio			—	—
Cobitidae				
Noemacheilus barbatulus	—			
Siluridae				
Silurus glanis			—	—
Anguillidae				
Anguilla anguilla		—	—	—
Gadidae				
Lota lota				—
Percidae				
Stizostedion lucioperca			—	—
Perca fluviatilis	—	—	—	—
Cottidae				
Cottus gobio	—	—	—	—
Number of species	6	9	17	17

any notable effect on the fish populations, which increased in density through 1967.

Species Composition

Before damming, Klíčava Brook contained (Table 3) the lamprey (*Lampetra planeri*), the minnow (*Phoxinus phoxinus*), the sculpin (*Cottus gobio*), the stone loach (*Noemacheilus barbatulus*), the stream form of brown trout (*Salmo trutta fario*), and the perch (Oliva 1949). The perch was not abundant. Other fishes also appeared in the brook after heavy floods. Shortly after filling, five other species were found that apparently had missed Oliva's sampling (Holčík 1970). Their numbers, however, were negligible.

In the year after the reservoir was full, nine species of fishes were recorded (Table 3). The native lamprey and the stone loach were already absent. The minnow and the sculpin persisted longer but disappeared after 1964. The brown trout population changed into the lake form *S. trutta lacustris* during the first 2 yr after the reservoir filling (see Frank 1959; Holčík 1965;

and Holčík and Bastl 1970). The trout population was low and remained low in spite of the stocking. The isolation of inlets by construction of filtering dams and the lack of suitable spawning grounds were responsible for the gradual decline or loss of the above species.

The number of species increased to 16 from 1962 to 1975 (Table 3). As only huchens and rainbow trout (*Salmo gairdneri*) were intentionally introduced, the appearance of other species, mainly cyprinids, must be ascribed to immigration from upstream ponds during floods. For example, in 1961 the water of inlets was higher than the crowns of filtering dams. Alternatively, fertilized eggs may have been transferred by water fowl, or people having access to the reservoir may have arbitrarily and illegally introduced species. However, only six fishes were important on the basis of abundance in experimental catches: the perch, the roach, the rudd (*Scardinius erythrophthalmus*), the chub (*Leuciscus cephalus*), the tench (*Tinca tinca*), and the northern pike. After 1967 the carp (*Cyprinus carpio*) and the pikeperch also reached sufficiently abundant densities that their populations could be estimated. All other species probably had a negligible role in the ecosystem.

Density, Biomass, and Production

Changes in population density and biomass of fishes can be followed from 1957 to 1972 (Table 4), because population estimates were made more or less regularly by the mark–recapture method (Oliva and Holčík 1965; Holčík 1970; Pivnička 1971; Holčík and Pivnička 1972, 1975). My values of density and biomass in 1971 and 1972 were slightly different from those of Holčík and Pivnička (1972) owing to minor corrections and to differences in definition of reservoir area. Holčík and Pivnička related all calculations to a uniform area of 67 ha, whereas I used actual areas for each year. Methods are given in Holčík (1970), Holčík and Pivnička (1975), and Pivnička and Švátora (1977). Although values in Table 4 are for only 6–8 species, they most likely represent the actual status of the entire fish community, because other species were negligible.

Fish biomass (Table 4) rose from 65 kg/ha in 1957 to a maximum of 236 kg/ha in 1967. Because the reservoir was full by 1955, 2 yr before our first estimate, the time interval to obtain maximum biomass was 12 yr. After 1968 the biomass decreased gradually until 1971, when it reached 166 kg/ha. In 1972 it rose slightly to about the value for 1970. Density fluctuated more than biomass with a peak in 1964 (Table 4), when there were more than 10,000 fish/ha. After 1964 density fluctuated between 1700 and 5100 fish/ha with no regular trend. Also, the highest estimate of production ($P = G\bar{B}$) was in 1964 (Table 4). Later it fluctuated between 51 and 102 kg/ha. Actual abundance and production were certainly higher, because with the exception of perch, roach, and chub, for which numbers of yearlings were calculated, only specimens older than 2 yr were included in the estimates.

Substantial differences were observed in historical changes for each species (Table 4). In 1957 perch predominated in the biomass. From 1964 to 1972 the roach was the most important species as the biomasses and abundances of perch as well as of northern pike and tench decreased. Chub and rudd continued to increase. Between 1968 and 1972 the fish community apparently reached an equilibrium and each species occupied a more or less fixed place. Generally, the fish stocks underwent changes similar to those in most other European reservoirs (Mikheev and Prokhorova 1952; Wajdowicz 1964; Holčík 1966), i.e. phytophils, which flourish in the initial stage of reservoir existence, were replaced by plastic species (Holčík and Hruška 1966), i.e. phytolithophils (Balon 1975). The only exceptions were the increases in rudd, which can be explained by the increased density of aquatic plants, and in chub by reproductive adaptations (Pivnička 1971). However, the decline in perch, despite their ecological similarity to roach, can be explained by specific features of their population dynamics, as explained below.

Predation

Except for uncommon sheatfish (*Silurus glanis*), the northern pike, the pikeperch, and the perch were the only piscivores in the reservoir. Though pike and pikeperch are predators from the early stages of their lives, only the larger perch, age-group V (i.e. >170 mm SL) and older, were considered to be piscivores. Perch shorter than 170 mm SL ate zooplankton almost exclusively. In perch from 170 to 200 mm SL fish increased in the diet, and those longer than 250 mm ate fish almost exclusively (Lohniský 1960, 1967). The chub may also be a predator, but most authors (Cragg-Hine 1963; Leeming 1963; Gyurkó and Nagy 1965, 1971) consider it an omnivore. In my analysis, I do not consider chub as a predator on fish.

On the basis of the ratio of the total weight of forage fish to that of carnivores (F/C index) (Swingle 1950), the fish community can be considered to have been in balance only in 1964 (Table 4). On the basis of Swingle's criterion, the

TABLE 4. Densities, biomass, and production of total fish population in Klíčava Reservoir and density and biomass estimates for piscivores, forage fishes, and individual species 2 yr after filling (1957) and later years (1964, 1967–72). Calculated with mean surface areas for individual years. Data from Oliva and Holčík (1965), Holčík (1970), Pivnička (1971), and Holčík and Pivnička (1972, 1975).

	1957	1964	1967	1968	1969	1970	1971	1972
All Species								
Density	1,110	10,749	3,284	5,076	2,671	1,743	3,130	3,677
Biomass (kg/ha)	65	207	236	187	180	170	166	170
Production (kg/ha)	25	136	102	63	93	73	51	81
Piscivores								
Density (number /ha)	?	130	12	19	38	33	61	79
Biomass (kg/ha)	26.3	19.9	4.2	3.3	6.3	6.3	8.5	11.5
(% of all species)	40.2	9.6	1.8	1.8	3.4	3.7	5.1	6.6
Forage fishes								
Biomass (kg/ha)	39	187	232	184	174	164	158	159
Pikeperch								
Density (number/ha)	—	—	1.3	0.5	1.1	1.7	1.7	1.7
Biomass (% of all species)	—	—	—	0.2	0.3	0.6	0.6	0.7
(% of piscivores)	—	—	—	8.6	10.0	15.3	11.6	9.6
Piscivorous perch								
Density (number/ha)	47	126	9	18	35	30	58	75
Biomass (% all species)	22.1	7.6	0.7	0.9	1.7	1.6	2.9	4.6
(% of piscivores)	54.9	78.9	38.4	47.6	49.0	43.7	57.0	64.4
Forage perch								
Biomass (kg/ha)	22.6	21.3	13.7	14.9	14.1	14.7	8.7	9.4
(% all species)	34.6	10.3	5.8	8.0	7.8	8.6	5.2	5.5
Northern pike								
Density (number/ha)	8.7	3.7	1.6	0.9	1.7	1.7	1.7	1.7
Biomass (% of all species)	17.8	2.0	1.1	0.8	1.4	1.6	1.6	1.8
(% of piscivores)	44.2	21.1	61.7	43.8	41.0	41.0	31.4	26.0
Roach								
Biomass (kg/ha)	—	143	195	135	136	122	120	121
(% of all species)	12.6	69.3	82.7	72.0	72.0	71.3	72.2	71.1
Chub								
Biomass (kg/ha)	2.9	17.6	19.0	19.7	18.2	13.3	14.0	11.4
(% of all species)	4.9	8.5	8.1	10.5	9.6	7.8	8.4	6.7
Tench								
Biomass (kg/ha)	4.5	1.7	0.7	0.8	0.7	0.7	0.7	0.8
(% of all species)	6.9	0.8	0.3	0.5	0.4	0.4	0.4	0.5
Rudd								
Biomass (kg/ha)	0.9	2.9	3.4	3.9	3.7	4.3	4.5	5.0
(% of all species)	1.3	1.4	1.4	2.1	2.0	2.5	2.7	2.9
Carp								
Biomass (kg/ha)	—	—	—	9.7	1.0	9.7	10.0	11.2
(% of all species)	—	—	—	5.2	5.2	5.7	6.1	6.6

population had too many predators in 1957 and too many forage fish after 1967. The piscivores formed about 40% of the fish biomass in 1957 (Table 4), decreased from 1957 to 1967 and increased gradually beginning in 1969.

Because the fish biomass decreased while the percentage of piscivores increased from 1968 to 1972, I tried to find if there was a relation between these variables. When the total fish biomass was plotted against percentage of piscivores by weight in the population (Fig. 2), different relations were apparent for the periods 1964–67 and 1968–72. In both periods coefficients were negative with $r = -0.80$ for 1968–72 and $r = -0.999$ for 1957, 1964, and 1967. Similarly, the biomasses of piscivores and forage fish from

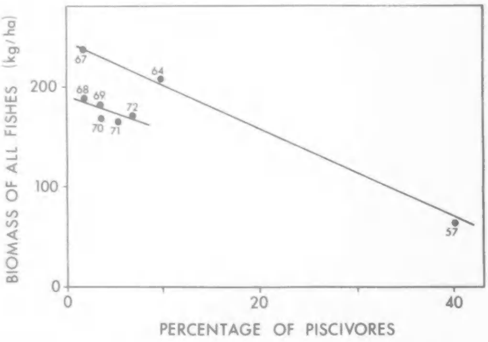

FIG. 2. Relation between total fish biomass and percentage of piscivores in Klíčava Reservoir for 1957, 1964, and 1967 (upper line) and 1968 to 1972 (lower line). Data are from Table 4.

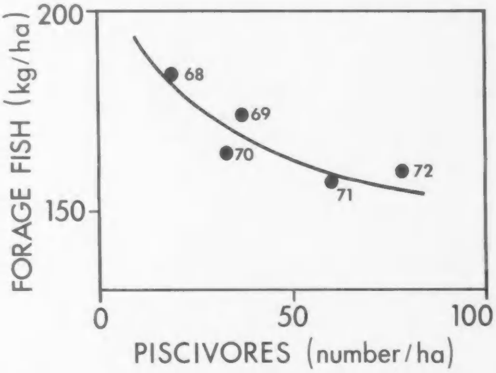

FIG. 3. Relation between biomass of forage fish and the number of piscivores in Klíčava Reservoir, 1968–72. Data are from Table 4.

1968 to 1972 were negatively correlated, $r = -0.87$. Oliva (1957) found that for fish populations of the Elbe region predator density seemed to be more important than their biomass. Therefore I plotted the number of predators against the total weight of forage fish from 1968 to 1972 (Fig. 3) and obtained an exponential relationship that was statistically significant ($r = -0.89$, $n = 5$).

In an attempt to deduce the influence of a particular species of predator on the forage fish I calculated the linear correlation between the density of each piscivore and the biomass of prey species (Table 5). In each case the biomass of prey decreased with the increasing density of the piscivore. The greatest effect on total forage fish seemed to be from the pikeperch because the correlation was highest for this species. The statistically significant correlation coefficients were between pikeperch and roach, pikeperch and chub, and perch and forage perch. None of the correlations with northern pike was significant, nor was any with rudd as prey. Piscivores were positively correlated (northern pike and pikeperch, $r = +0.90^{**}$; perch and pikeperch, $r = +0.83$; and northern pike and perch, $r = +0.82$). The interpretation of these findings may be as follows: (1) increasing density of piscivorous perch reduced the biomass of forage perch, (2) pikeperch reduced roach and chub, (3) rudd were only slightly reduced, if at all, by predation, and (4) northern pike did not have important effects on prey species in comparison with perch and pikeperch.

The above inferences agree with data on the diet of northern pike, perch, and pikeperch. Pike and pikeperch select the most abundant and available prey, whereas perch are highly cannibalistic (Dziekońska 1955; Fortunatova 1949; Antosiak 1958, 1963a; Popova 1965). Preferred foods of pikeperch and northern pike are roach and perch. Thus, I think that until 1960–64 the northern pike preyed primarily on perch and from 1965 to 1972 on roach, which became more abundant and available than perch (Table 4, also see Fig. 7). The importance of chub increased from 1964 to 1972 for both northern pike and pikeperch. At the time of writing the roach seems to be the most important food, followed by chub and perch. Perch have quite different habits from other piscivores. Lohniský (1960, 1967) found that the stomachs of piscivorous perch in the reservoir contained exclusively their own young, and a high degree of cannibalism also is known in more diverse fish faunas (e.g. Bogdanov 1959; Żuromska 1961; Vashkevichiute 1959; Lác 1962; Antosiak 1958, 1963b; Nümann 1973; Hartmann 1975; Vostradovský 1975). That the influence of piscivores on the population of rudd was slight or absent may be explained by their segregation in space. Rudd feed on macrophytes. In the Klíčava submersed vegetation such as *Ceratophyllum*, *Myriophyllum*, and *Potamogeton* spp. has developed since 1962. Since rudd were always caught close to shore, I think that they utilize vegetated areas as shelters.

It is remarkable that the decrease in the roach, and thus, in the entire fish stock, started after the introduction of the pikeperch. This confirms observations (Swärdson and Molin 1973) that pikeperch introductions negatively influence populations of other species of fish, including the roach and perch. The decline of the perch population from 1968 to 1972 may also be connected with the introduction of the pikeperch.

TABLE 5. Correlation coefficients between densities of piscivores and biomasses of forage fishes in Klíčava Reservoir based on 6–8 yr. Data from Table 4. (*$P \leq 0.05$; **$P \leq 0.01$.)

Piscivore density (number/ha)	Prey Biomass (kg/ha)				
	All forage fishes	Roach	Forage perch	Chub	Rudd
Pikeperch	−0.98**	−0.90*	−0.67	−0.97**	+0.80
Perch	−0.88*	−0.68	−0.92*	−0.78	+0.86
Northern pike	−0.86	−0.62	−0.55	−0.79	+0.56

Although my conclusions need further observations for verification, the decrease of fish biomass from 1968 to 1972 appears to result from increased densities of piscivores. This agrees with the results from Cultus Lake (Foerster and Ricker 1941), where a decrease in predators correlated with increasing density of their prey (*Oncorhynchus nerka*) and those of Bonar (1977), who observed that an increasing predator density was accompanied by decreasing total catch of fish.

Effect of Perch Cannibalism on its Own Population

Cannibalism by perch is well known, but quantitative studies have been on water bodies in which perch was the only species (Eschmeyer 1937, 1938; Alm 1946; Burmakin 1961; Źuromska 1961; Burmakin and Zhakov 1961; Rudenko 1962). In such lakes structures of perch were not pyramidal because younger fish were rare in respect to older fish. Eschmeyer was the first to express the opinion that "most of the young perch of those lakes had been eaten by the larger fish" (1938:629) and that "a definite cycle with respect to age and size composition of the stock normally occurred in the population" (1937:626). According to him (1937:626), "In such a cycle one age group would be very abundant, would keep down the two following age groups by eating the eggs of young, would die of starvation in its third year (in the quoted lake only 3 age groups were present — note of J. H.), and, in dying, would make possible the survival of another group." Independently Burmakin and Zhakov (1961) and Źuromska (1961) assumed that the unusual age composition in perch lakes was owing to cannibalism. Later, Menshutkin and Zhakov (1964) developed a model for such populations and demonstrated that the cannibalism is responsible for the disappearance of young age-groups and that the age structure of perch populations changes in regular cycles.

Nonpyramidal age structures for perch also were observed in the Klíčava and again explained mainly by cannibalism (Holčík 1969a). Data gathered by Pivnička (1971) and Švátora (1974) on the age composition and density make a more complete evaluation possible. First, as noted, increased densities of piscivorous perch reduced the biomass of forage perch. Two distinct phases in the relation between piscivorous and forage perch were apparent (Fig. 4). One, from 1967 to 1971, was inverse, whereas the other, for 1963–66 and 1971 and 1972, was directly proportional (Fig. 4). The maximum size of perch eaten was 30% of the length of the piscivorous perch (Horosze-

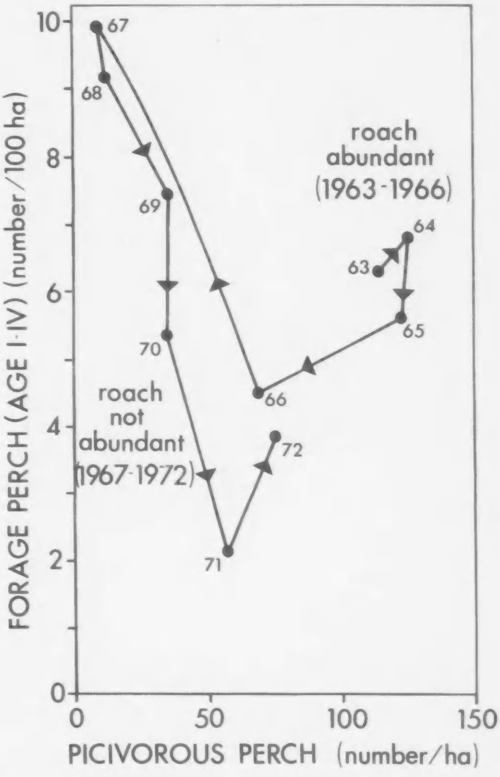

FIG. 4. Relation between forage perch and piscivorous perch, 1963–72. Data are from Table 4.

wicz 1964). Larger ones were unavailable. Thus, only the perch of age-group I and a negligible part of age-group II can be affected by cannibalism. For example, from 1967 to 1971 the density of age-group I was significantly correlated with the density of piscivorous perch ($r = -0.97^*$, $n = 5$), but that of age-group II was not ($r = -0.33$, $n = 5$). Fry and fingerlings were also eaten by older perch and their densities should be inversely related to the density of piscivorous perch. I do not have data on the number of fry and/or fingerlings, but number of piscivorous perch in one year can be compared with the number of age-group I in the next year (Fig. 5). The time course of lines and correlation coefficients in Fig. 5 suggests that in the early years cannibalism probably occurred but did not reduce the young perch as low as it did in the later years. The existence of two dependence levels can be explained as follows (Pivnička and Švátora 1976, 1977).

In the early years the fish density was high. Numbers of adult perch were so high that a lower percentage of females spawned and they had reduced fecundity. In this period predation by piscivorous perch on its own young was probably low because roach fry were so abundant. Roach is as important as young perch in their diets (Antosiak 1963b; Vostradovský 1975). The average number of roach in age-group I from 1963 to 1966 can be estimated at 3500/ha from Pivnička (1971). From 1967 to 1970 the density of roach of age-group I decreased to about 700/ha. At the same time the density of piscivorous perch, which reached a critically low level in 1967, slowly increased due to recruitment of year-classes hatched in 1962 and earlier, but did not reach the same density as in the early years. Since the density of roach fingerlings was 5 times lower than in the early years, piscivorous perch ate their own young more intensively. The positions of the data points for 1971 (Fig. 5) and 1972 (Fig. 4) suggest that in 1970 a large year-class was formed and that the number of piscivorous perch was sufficient for a new cycle to begin.

The correspondence between the increased cannibalism of perch and decreased density of the roach fry follows also from observations of Vostradovský (1975) in the Želivka Reservoir. There, from 1972 to 1975 the percentage occurrence of perch fry in piscivorous perch stomachs decreased from 84 to 30% while roach fry increased from 16 to 50% in accord with an increased density of roach. The reason for high cannibalism of perch is unclear. The specialized behavior (Deelder 1951) of perch in hunting for prey may cause only certain species among the potential prey to be available. Roach fry and fingerlings seem to be less available than the young perch when the densities of the two prey are the same. The bigger surface of *Corpus cerebelli* in roach (Bastl and Kirka 1957) than in perch (Kirka 1963) suggests that roach are more mobile than perch of the same size and thus more able to escape a predator. Another indication of higher mobility in roach than in perch is seen in their greater resistance to current. Holčík (1966) found roach in streams with high slope gradient. Fast growth of roach in the Klíčava may also help explain why it is less available than the perch (Holčík 1967, 1969a, b).

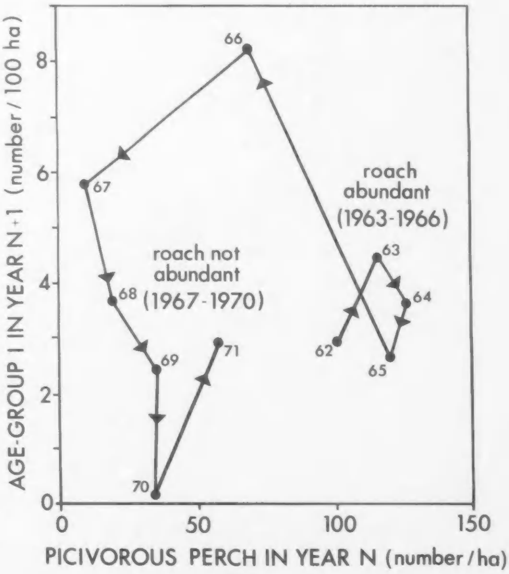

FIG. 5. Relation between numbers of piscivorous perch and numbers of age-group I perch the following years in Klíčava Reservoir, 1962–71. Data are from Table 4 in part.

Observations of the two levels for the relation between the piscivorous and forage perch agree well with the model developed for a monospecific population of perch in Tyulenie Lake by Menshutkin and Zhakov (1964) and Menshutkin (1971). In the Klíčava cyclic fluctuations in population structure occurred too (Fig. 6). Immature fish were abundant when the density of mature or piscivorous perch was lowest, just as in Tyulenie Lake. The year 1966 seemed to end the initial irregular "wandering" of the ecosystem's population structure, while later years (1967 to 1971) resembled the first regular cycle passing into a second one in 1972. Thus, I conclude that can-

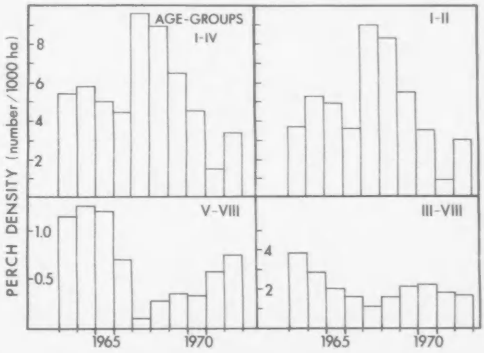

FIG. 6. Changes in the densities of forage perch (age-groups I–IV) and piscivorous perch (age-groups V–VIII), on the left, and juvenile perch (age-groups I–II) and mature perch (age-groups III–VIII), on the right, in Klíčava Reservoir, 1963–72. Data are from Table 4 in part.

nibalism by perch causes cyclical changes in density and age composition of its own population in complex communities just as Menshutkin found for simple communities.

Relation between Fish Stock and Feeding

Fish biomass increased from 1957 to 1964 even though the biomass of zooplankton had decreased (Fig. 7). A decline in zooplankton as the main food source would be expected to result in decreased fish biomass (Nikolsky 1974; Menshutkin 1971). However, the zooplankton decline can be interpreted to result from the increased biomass of fishes. Though inertia must have occurred while the equilibrium between the zooplankton and fish abundance was being reached, the fish biomass continued to rise in the 10 yr following the precipitous decline in zooplankton. Also, from 1958 to 1970 the zooplankton biomass fluctuated more or less regularly and the decline of fish biomass was presumably due to increased fish predation. Since I found no correlation between the biomass of zooplankton and the amount of phosphorus or nitrogen, I examine below the relation between zooplankton and fish abundance.

Zooplankton biomass was only weakly correlated with total fish biomass ($r = -0.58$, $n = 6$) and forage fish biomass ($r = -0.59$, $n = 6$) for years with data (Fig. 7). The relation was a little stronger when data for 1957, when phosphorus was still high, were omitted ($r = -0.68$ and $r = -0.76$). I think the decline of zooplankton was due mainly to grazing by zooplanktivorous fishes. These were primarily perch of age-groups 0–III and the roach of age-groups 0–II, i.e. roach <100 mm SL (Hruška 1956; Nagy 1974). To utilize the zooplankton data after 1956 and for years when the fish population was not estimated, the densities (Table 6) of perch of age-groups I, II, and III and of roach of age-groups I and II were estimated after Holčík and Pivnička (1975).

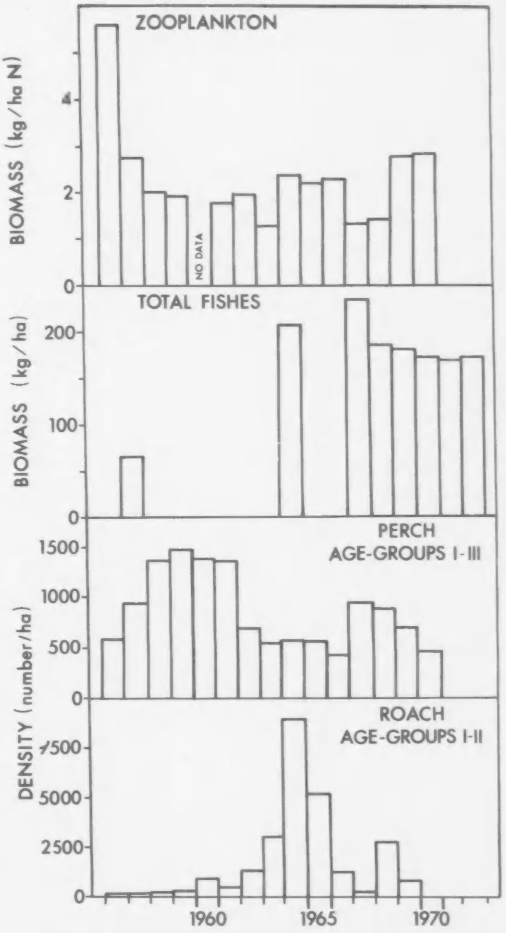

FIG. 7. Biomasses of zooplankton and all fishes and densities of perch (age-groups I–III) and roach (age-group I–II) in Klíčava Reservoir 1956–73. Data are from Tables 4 and 6.

The initial decline in zooplankton biomass correlated closely with the increase in young perch from 1956 to 1959 (Fig. 7). After 1960 the relation is not as clear, but, again, zooplankton was higher when perch were lower and vice versa. For example, the increase in zooplanktivorous perch in 1967 and 1968 corresponded with lower biomasses of zooplankton. Young

TABLE 6. Densities (number/ha) of perch of age-groups I–III and roach of age-groups I–II and biomasses (kg/ha nitrogen) of zooplankton in Klíčava Reservoir, 1956–70. (Sources — see acknowledgments plus text.)

	Density of zooplanktivores		
Year	Perch	Roach	Zooplankton biomass
1956	588	28	5.63
1957	932	80	2.78
1958	1388	212	2.00
1959	1494	276	1.89
1960	1390	907	—
1961	1365	427	1.76
1962	675	1304	1.95
1963	541	2955	1.27
1964	579	8876	2.37
1965	538	5185	2.19
1966	425	1174	2.28
1967	957	225	1.35
1968	877	2778	1.40
1969	692	859	2.78
1970	454	48	2.86

roach appeared to have no influence on the biomass of zooplankton (Fig. 7). The large increase in roach density in 1964 and 1965, for example, coincided with an increase rather than a decrease in zooplankton. Correlation coefficients between roach density and zooplankton biomass were insignificant. The roach has a catholic diet composed of zooplankton and phytoplankton, and the phytoplankton was probably more important in seasons when fry and yearling densities were high, such as in 1964 and 1965. Zooplankton biomass was then much more influenced by the perch than by roach (Fig. 7). The depletion of zooplankton biomass and the change in its species composition was most marked during the early years of the reservoir, when the perch population rapidly increased. The relation with perch at a lower level in later years may be explained by the changes in species composition of zooplankton. Larger species were replaced by smaller ones with higher turnover rates and more rapid renewal of biomass. Thus, the effect of grazing on zooplankton was marked as in the early years, when the larger forms of zooplankton predominated.

These findings support the suggestions of Řeháčková-Rozmajzlová (1966) and Brandl (1974) that the decline in zooplankton biomass and disappearance of larger zooplankters in the early years of the Klíčava Reservoir were affected by increase in densities of fishes. The negative relation between fish and the biomasses of zooplankton and benthos was demonstrated by Vladimirova (1963) and Burmakin (1963) in lakes which were treated with poison to kill fishes, then fertilized, and later stocked with *Coregonus peled* and carp. After the introduction of fish, the biomasses of zooplankton and benthos dropped substantially and the larger zooplankton species were replaced by smaller ones. In fenced enclosures without fish the total biomass of net zooplankton, mainly cladocerans and copepods, increased considerably (Vranovský 1965). In control areas inhabited by fishes the biomass of zooplankton was composed mostly of rotifers.

The period 1955 to 1969 in the Klíčava Reservoir resembles the period between the poisoning and restocking of the Russian lakes quoted above, i.e. a short transition stage before the fish population developed. The changes in the zooplankton biomass cannot be explained by the changes in nutrients. Nitrogen content did not change between 1955 and 1964 and the phosphorus content was higher only in 1957 and 1958 (Fig. 1).

Also, in the Klíčava the importance of zooplankton in the diet of fish is much greater than that of benthos (Hrbáček 1962). According to V. Hruška (personal communication) the benthos in the Klíčava is not abundant (no quantitative investigations were made, however) and may be relatively unavailable to fishes. This would follow from the vertical distribution of fishes in the Klíčava determined by echo sounding (Straškraba 1974). Fishes were concentrated between 4 and 13 m and only single specimens were recorded deeper in water below the epilimnion.

Conclusion

Fish population changes in Klíčava Reservoir from 1957 to 1972 were analogous to those in other man-made lakes of similar type. Soon after filling, the lithophils disappeared or significantly decreased. They were replaced by phytophils and then by plastic indifferents which became dominant. The decreasing biomass of fish, after carrying capacity of the reservoir is reached, results from increased predation and not from a decline in productivity of the reservoir. Zooplankton biomass also declines and its species composition changes because of increases in zooplanktivores, primarily perch, in the early years of the reservoir. The synchronous action of predation on forage fish by piscivores helps to stabilize the zooplankton biomass soon after the initial decline. This antagonistic relationship between prey and predators seems to be one of the main mechanisms responsible for the balance between the food resources and fish stocks. Among predators the pikeperch seems to be more effective than the northern pike. The decline of the perch population is due to interaction of several factors, namely a high rate of cannibalism and decreasing fecundity with increasing population density, and the influence of other species, such as predation by pikeperch and competition with and predation from roach. Roach eat eggs and fry of other species (Cherfas 1949; Shutov 1962; Eltsova 1976), and perch larvae are very vulnerable when they are planktonic: Řepa (1965) found perch larvae in the Klíčava at depths of 2–5 m in the pelagial. On the other hand, the perch seems rather autonomous because it controls its own density in accord with existing food resources. The perch functions in the fish community like three species: part of its population is zooplanktivorous, part feeds on benthos, and the third part, composed mainly of females, is predatory. The intense cannibalism by perch is probably due to the high availability of its own young compared with other species. This habit is responsible for cyclical changes in the density and the structure of its population.

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Population Dynamics of Yellow Perch (*Perca flavescens*), Sauger (*Stizostedion canadense*), and Walleye (*S. vitreum vitreum*) in Four Main Stem Missouri River Reservoirs[1]

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NELSON, W. R., AND C. H. WALBURG. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River reservoirs. J. Fish. Res. Board Can. 34: 1748–1763.

Percid populations have generally increased in abundance relative to other groups of fishes in the 15–25 yr four large reservoirs have been operational on the Missouri River in South Dakota. Saugers (*Stizostedion canadense*) were initially the most abundant percid, but their numbers gradually declined, probably because of the reduction in river spawning habitat and the increase in water clarity. Yellow perch (*Perca flavescens*) increased to high population levels as the reservoirs filled but later decreased in abundance. Walleye (*S. vitreum vitreum*) populations were the slowest to develop in the reservoirs, probably because of initial lack of suitable spawning habitat; they later became well established.

The yellow perch was one of the most important forage species in the reservoirs, and walleyes and saugers the primary predator and sport fishes. Sportfishing quality 15–25 yr after impoundment was good, but harvest remained low because of the large size of the reservoirs, inadequacy of facilities for anglers, and the relatively sparse human population. Reproductive success was the primary factor regulating the abundance of percids. Year-class strength was primarily determined by climatic rather than biological factors. Above-average precipitation presumably enhanced reproductive success, both directly by increasing the quantity and quality of spawning substrate through higher stream flows and water levels, and indirectly by providing a larger forage supply, thereby apparently reducing predation on young percids, as well as cannibalism.

Key words: Percidae, reservoirs, Missouri River, *Stizostedion*, *Perca*, population dynamics, ecology, precipitation, water level

NELSON, W. R., AND C. H. WALBURG. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River reservoirs. J. Fish. Res. Board Can. 34: 1748–1763.

Les populations de percidés ont en général augmenté par rapport aux autres groupes de poissons au cours des 15 à 25 ans durant lesquels quatre grands réservoirs ont été opérationnels sur le fleuve Missouri dans le Dakota-Sud. Les dorés noirs (*Stizostedion canadense*) étaient au début le percidé le plus abondant, mais leurs nombres ont diminué graduellement, probablement à cause de la diminution de l'habitat de fraie en rivière et l'augmentation de la clarté de l'eau. La perchaude (*Perca flavescens*) atteignit de hauts niveaux de population à mesure que les réservoirs se remplirent, mais par la suite diminua d'abondance. Les populations de dorés jaunes (*S. vitreum vitreum*) furent les plus lentes à se développer dans les réservoirs, probablement à cause du manque de frayères convenables au début; elles devinrent bien établies par la suite.

La perchaude est une des espèces fourragères les plus importantes dans les réservoirs, alors que le doré jaune et le doré noir sont des prédateurs primaires et des poissons de sport. La pêche sportive, 15–25 ans après le remplissage des réservoirs, est de bonne qualité, mais la récolte demeure faible à cause de la grandeur des réservoirs, d'installations inadéquates pour les pêcheurs à la ligne et d'un population humaine relativement éparse. Le principal facteur de contrôle de l'abondance des percidés est le succès de la reproduction. L'abondance d'une classe d'âge est déterminée par des facteurs climatiques plutôt que biologiques. Une précipitation

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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dépassant la moyenne favorise probablement la reproduction, à la fois directement, en augmentant la quantité et la qualité du substrat des frayères, grâce à un débit et à des niveaux d'eau accrus, et indirectement, en augmentant les approvisionnements d'espèces fourragères, réduisant de cette façon, semble-t-il, la prédation sur les jeunes percidés ainsi que le cannibalisme.

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In this review, we describe the development of the yellow perch, sauger, and walleye populations in the lower four of six main stem reservoirs on the upper Missouri River: Lewis and Clark Lake, Lake Francis Case, Lake Sharpe, and Lake Oahe. The pertinent geological and climatic characteristics of the basin as well as the physical characteristics and water management of the individual reservoirs are described. The interaction of environmental variables with time was reflected in the changing abundance and distribution of these percids in each reservoir.

Construction of dams has transformed the once uncontrolled, silt-laden Missouri River into a series of large reservoirs with regulated elevations and flows. Fish in the river were virtually unexploited; the channel catfish (*Ictalurus punctatus*) was the primary species harvested. After impoundment an excellent sport fishery developed, originally for northern pike (*Esox lucius*) and saugers (*Stizostedion canadense*), and later for walleyes (*S. v. vitreum*). Commercial fishing for these species is unlawful, and the sportfishing pressure is light because of large size of the reservoirs, poor access, and sparse human population.

Description of Missouri River Basin

Geology and land use — The Missouri River delineates the southern boundary of Pleistocene glaciation. Till and glacial deposits predominate on the northern or eastern banks, and Cretaceous and Paleocene sedimentary deposits on the southern or western banks (Rothrock 1943). These sedimentary deposits of shale, sandstone, and chalk have formed soils that are easily eroded. Consequently, the older southern and western shores are more rugged and bisected by more tributary streams than are the northern and eastern shores.

The fine soils derived from the sedimentary deposits (clay, silt loam, loam, and sandy loam) cause high turbidities in unimpounded stretches of the river and tributary streams, and large amounts of these soils are deposited annually where the streams enter the impoundments. The combination of wind, fluctuating water levels, and soil types has caused extensive bank slumping, which has increased turbidity and deposition of sediments in the reservoirs.

The basin is mostly an agricultural area, with little industrial development. Grazing and small-grain farming predominate along the western and southern boundary of the river, and row crop and small-grain farming along the eastern and northern boundary.

Climate — The climate is semiarid, with hot summers, cold winters, and much wind. Annual precipitation decreases from an average of 65 cm at Yankton, South Dakota, to 40 cm at Bismarck, North Dakota. Most precipitation occurs in the spring, with the maximum usually in June. Annual snowfall averages about 75 cm, but snow rarely accumulates because of thaws between the frequent light snowfalls.

Temperatures range from over 40°C in summer to −35°C in winter. Mean temperature at Yankton, South Dakota, is about 24°C in July and −12°C in January; temperatures at Bismarck, North Dakota, average about 2°C lower. Wind velocity averages more than 13 km/h annually, and velocities exceeding 80 km/h are common; velocities are highest in spring and lowest in summer. Winds are generally southeasterly in summer and northwesterly during the rest of the year.

Description of the Reservoirs

Of the approximately 800 km of Missouri River from Gavins Point Dam to the upper end of Lake Oahe, only 85 km remain unimpounded (Fig. 1). This stretch extends from the upper end of Lewis and Clark Lake to Fort Randall Dam. An additional 139 km of unimpounded river flows from Garrison Dam to the upper end of Lake Oahe. Characteristics of the four reservoirs are given in Table 1.

Common attributes — Trees and bushes were abundant in the valleys of the river and its tributaries, and few were removed during construction of the

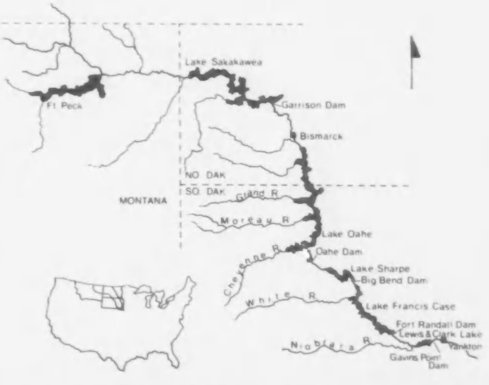

FIG. 1. Missouri River main stem reservoirs.

TABLE 1. Selected physical characteristics of four Missouri River main stem reservoirs at base of flood control.

Reservoir	Dam closed (yr)	Operating level attained (yr)	Surface area (10^3ha)	Volume (10^9m^3)	Depth	
					Maximum (m)	Mean (m)
Lewis & Clark	1955	1956	10.5	0.5	16.7	5.0
Francis Case	1952	1957	32.0	4.1	42.6	15.2
Sharpe	1963	1965	23.1	2.3	23.7	9.5
Oahe	1958	1967	126.8	23.7	60.8	19.2

Reservoir	Length (km)	Mean width (km)	Shoreline		Mean annual water level fluctuation (m)	Water exchange rate (yr)
			Length (km)	Development		
Lewis & Clark	40	3.4	145	2.1	1.1	0.03
Francis Case	172	1.3	870	11.9	6.9	0.5
Sharpe	129	1.6	322	5.1	0.6	0.1
Oahe	372	3.9	3,623	27.4	3.8	1.1

reservoirs. Consequently, trees and brush protrude above the water surface in the upper reaches of the reservoirs and tributary embayments. Ice and wind action reduce the number of trees each year and silt is gradually covering the brush. Aquatic vegetation is nearly nonexistent in the reservoirs, due to wind action and fluctuating water levels. Terrestrial revegetation along the intermittently flooded shoreline is retarded by water level fluctuation, late summer drawdown, wave action, lack of soil aeration, and cattle grazing (Vanderveen 1973).

Turbidity is lowest near the dams and increases upstream. Lewis and Clark Lake is the most turbid because of its small area and shallowness, and the deposition of silt from the Niobrara and Missouri Rivers. Secchi disk readings above Gavins Point Dam average about 0.5 m and rarely exceed 1.0 m; readings in Lakes Francis Case and Sharpe average about 1.5 m and sometimes reach 2.5 m (Benson 1968). Although readings above Oahe Dam average 3.5 m (maximums exceed 6.0 m), readings of 2 cm are common in the upper reaches of bays, and in the open lake during periods of high winds.

Dissolved oxygen concentrations are usually near saturation at all depths in the reservoirs, including the hypolimnetic waters of Lake Oahe (Selgeby and Jones 1974). Evidently oxygen demand is low because few organic materials are present and these are continually being covered with silt.

Lewis and Clark Lake — The primary function of Lewis and Clark is the reregulation of flows from Fort Randall Dam. The lake is characterized by rapid exchange of water; exchange rate varies from 3 to 12 days, depending on year and season. Much of the reservoir is bounded by steep bluffs composed of Niobrara chalk overlain with alluvium. The shoreline is essentially straight except for narrow bays at the mouths of six small, intermittent tributary streams. The reservoir bottom is largely mud and silt (deposited by the Niobrara and Missouri Rivers), with few areas of sand and gravel. Hydrographic and physical–chemical features of the reservoir were reported by Cowell (1967).

Lake Francis Case — Lake Francis Case has steeply sloping shores of clay, clay loam, and exposed glacial till. There are numerous small bays at the mouths of intermittent streams and ravines, but no large embayments. The only significant tributary is the White River, an extremely turbid stream. The water rarely stratifies thermally or chemically except for short periods following several days of calm weather.

The lake is drawn down each fall to provide storage for water released from upstream reservoirs for winter generation of hydroelectric power. The drawdown was 6–14 m during 1956–70, but was reduced to 6–7 m in 1971–75. This drawdown has a detrimental effect on the benthos and periphyton in the reservoir (Cowell and Hudson 1967; Claflin 1968; Benson and Hudson 1975); the effect on the fish population has not been determined. Physical and chemical data on the reservoir were published by Benson (1968), Selgeby (1968), Cowell (1970), and Martin and Novotny (1975).

Lake Sharpe — The primary function of Lake Sharpe is power production and reregulation of discharges from Oahe Dam; little storage capacity is allocated for flood control. Water level is stable throughout the year, but the water exchange rate is relatively high. The rapid exchange rate, combined with the relatively low temperature of the water discharged from Oahe Dam, has prevented the formation of a thermocline.

Lake Sharpe was the only reservoir of the four that had rubble shorelines formed by outcrops of glacial till when it was filled. It has few bays or protected areas. Because tributaries are few and small and the inflow water from Lake Oahe is clear, little siltation occurs.

Lake Oahe — Lake Oahe was constructed for flood control and multiple use. In the seasonal cycle of operation followed in the mid-1970s, water level was near the base for flood control in early spring, rose through mid-summer, fell below the base for flood control by winter, and rose to the base during the winter. In 1968–75, water level fluctuations (due mainly to annual variations in runoff) have varied between 2.2 and 5.4 m and averaged 3.6 m.

Three large tributaries — the Cheyenne, Moreau, and Grand rivers — enter Lake Oahe from the west. These streams and numerous smaller tributaries, also mostly along the west shore, have created many embayments that greatly increase shoreline length. Siltation in the headwaters of these embayments is extensive and the accumulation increases annually.

Thermal stratification normally extends from June through September in about the lower two-thirds of the reservoir; duration decreases with increasing distance upstream from the dam. The depth of the metalimnion varies with distance from the dam, wind conditions, and water discharge (June 1974).

Sampling Methods and Gear

Studies of the fish populations in these reservoirs were initiated by the South Dakota Department of Game, Fish and Parks in 1954 and in 1962, North Central Reservoir Investigations of the U.S. Fish and Wildlife Service was formed to continue the work.

Standard sampling gears have been 0.5-m plankton nets (760 μm bar mesh) for capturing embryos and larvae, shoreline seines (0.6 cm bar mesh) for assessing apparent reproductive success, and variable mesh gill nets for assessing adult populations. Shoreline seines used by State personnel were 12.2 m long and those used by Federal personnel were 30.5 m long. Experimental gill nets used by State personnel were 76.2 m long and consisted of five 15.24-m panels of graded mesh size — 1.9, 2.5, 3.2, 3.8, and 5.1 cm (bar mesh). Gill nets used by Federal personnel were similar except that they contained two additional panels, of 6.4- and 8.9-cm mesh.

Shoreline seining was generally done at locations throughout the reservoirs at 2-wk intervals during the summer. State personnel sampled the adult population during the summer while Federal personnel sampled during the fall in Lakes Oahe and Lewis and Clark and in the summer in Lakes Francis Case and Sharpe. Detailed descriptions of the various sampling methods have been published for Lewis and Clark Lake by Shields (1957a) and Walburg (1976); Lake Francis Case by Shields (1955) and Gasaway (1970); Lake Sharpe by Elrod and Hassler (1969); and Lake Oahe by Fogle (1961a) and Beckman and Elrod (1971). Methods of conducting creel censuses at Lake Francis Case and its tailwaters were described by Shields (1956) and at the tailwaters of Oahe Dam by Fogle (1961a); Schmidt (1975) described the creel census at Lake Sharpe.

Composition of Fish Population

The species composition and abundance of fish in the four reservoirs (Table 2) are a reflection of the populations originally present in the Missouri River and the adaptability of individual species to a reservoir environment. Exceptionally large year-classes of carp, bigmouth buffalo, smallmouth buffalo, and northern pike were produced during initial filling of the reservoirs and inundation of terrestrial vegetation. In later years, the relatively short-lived northern pike decreased markedly in abundance, but the other species continued to be abundant (Walburg and Nelson 1966; Gasaway 1970; Gable 1974). Nest-building species such as largemouth bass, black crappies, white crappies, and black bullheads also benefited from the change to a lakelike environment, but by the early 1970s sedimentation in the upper ends of the bays had all but eliminated largemouth bass and black bullheads and the abundance of crappies was greatly reduced (Siefert 1969; Beckman and Elrod 1971). Species with semibuoyant eggs, such as white bass, goldeye, and freshwater drum, generally established large populations, since they are unaffected by sedimentation or fluctuating water levels. The abundant channel catfish and river carpsuckers apparently spawn in the tributary streams and were not affected by changes in reservoir habitats.

Hybrids of saugers and walleyes are not uncommon in Lewis and Clark Lake. Hybridization probably occurs because the spawning area for these species is limited and the spawning seasons overlap. Hybrids have characteristics of both species but more closely resemble the female parent (Nelson 1968a). About 10% of the saugers and walleyes collected by gill net from Lewis and Clark Lake resembled hybrids. Probable hybrids observed in the other three impoundments represented less than 1% of the catch.

Gizzard shad, emerald shiners, and yellow perch comprise the primary forage species. Emerald shiner and gizzard shad populations declined in the mid-1970s. Gizzard shad reach the northern limit of their distribution in Lake Sharpe and no overwinter survival of young was documented there in 1967–75; small populations of adults were also present in the two downstream reservoirs. Abundance of minnow species (other than carp) decreased with the change from a river to a reservoir environment (Walburg 1976; June 1976).

Introductions of salmonids in the lower reaches of Lake Oahe have met with only limited success.

TABLE 2. Species composition and relative abundance of fishes in Missouri River reservoirs (Benson 1968; June 1976; Walburg 1976) in South Dakota 15 to 25 yr after impoundment (A = abundant; C = common; R = rare).

Common name	Scientific name	Lewis and Clark	Francis Case	Sharpe	Oahe
Pallid sturgeon	*Scaphirhynchus albus*	R	R	R	R
Shovelnose sturgeon	*S. platorynchus*	C	C	A	C
Paddlefish	*Polyodon spathula*	C	C	R	R
Shortnose gar	*Lepisosteus platostomus*	C	C	R	R
Gizzard shad	*Dorosoma cepedianum*	C	C	C	
Goldeye	*Hiodon alosoides*	C	A	C	A
Bonneville cisco	*Prosopium gemmiferum*[a]			R	
Rainbow trout	*Salmo gairdneri*[a]		R	C	R
Brown trout	*S. trutta*[a]			R	
Lake trout	*Salvelinus namaycush*[a]				
Kokanee salmon	*Oncorhynchus nerka*[a]			R	R
Coho salmon	*O. kisutch*[a,b]			R	R
Rainbow smelt	*Osmerus mordax*[b]			R	R
Northern pike	*Esox lucius*	R	R	R	R
Carp	*Cyprinus carpio*	A	C	A	A
Brassy minnow	*Hybognathus hankinsoni*			R	R
Silvery minnow	*H. nuchalis*	R	R	C	C
Plains minnow	*H. placitus*			R	R
Flathead chub	*Hybopsis gracilis*		R	R	R
Silver chub	*H. storeriana*	C			
Golden shiner	*Notemigonus crysoleucas*			R	R
Emerald shiner	*Notropis atherinoides*	A	A	A	A
Sand shiner	*N. stramineus*		R		
Spottail shiner	*N. hudsonius*[a,b]	R			C
Topeka shiner	*N. topeka*			R	R
Red shiner	*N. lutrensis*	C	C	C	
Bluntnose minnow	*Pimephales notatus*			R	R
Fathead minnow	*P. promelas*	R	R	C	C
Blacknose dace	*Rhinichthys atratulus*			R	R
Creek chub	*Semotilus atromaculatus*		R	R	R
Blue sucker	*Cycleptus elongatus*	R	R	R	R
Bigmouth buffalo	*Ictiobus cypinellus*	A	C	A	A
Smallmouth buffalo	*I. bubalus*	C	C	C	A
River carpsucker	*Carpiodes carpio*	A	A	A	A
Shorthead redhorse	*Moxostoma macrolepidotum*	C	R	C	C
White sucker	*Catostomus commersoni*	R	R	C	C
Black bullhead	*Ictalurus melas*	R	R	R	R
Channel catfish	*I. punctatus*	A	A	A	A
Blue catfish	*I. furcatus*	R	R	R	
Stonecat	*Noturus flavus*	R	R	R	R
Flathead catfish	*Pylodictis olivaris*	C	R	R	R
Burbot	*Lota lota*	R	R	R	R
Brook stickleback	*Culaea inconstans*			R	R
White bass	*Morone chrysops*[b,c]	A	C	C	C
Green sunfish	*Lepomis cyanellus*	R	R	R	R
Orangespotted sunfish	*L. humilis*	R	R	R	R
Bluegill	*L. macrochirus*	R	R	R	R
Largemouth bass	*Micropterus salmoides*	R	R	R	R
White crappie	*Pomoxis annularis*	C	C	C	C
Black crappie	*P. nigromaculatus*	C	C	C	C
Iowa darter	*Etheostoma exile*			R	R
Johnny darter	*E. nigrum*	R	R		R
Yellow perch	*Perca flavescens*	C	A	A	A
Sauger	*Stizostedion canadense*	A	C	C	C
Walleye	*S. vitreum vitreum*	C	A	A	A
Freshwater drum	*Aplodinotus grunniens*	A	C	C	C

[a] Introduced in Lake Oahe.
[b] Introduced in Lake Sakakawea.
[c] Introduced in Lewis and Clark Lake.

White bass were not originally present in this section of the Missouri River, but stockings in the late 1950s and early 1960s resulted in substantial populations in the reservoirs. Rainbow smelt were introduced in Lake Sakakawea in 1972; by 1974 they had reproduced successfully in Lake Oahe and in 1975 young were collected in Lake Sharpe.

Yellow Perch

Reproduction — The reproductive habits of yellow perch have only been investigated in Lakes Francis Case and Oahe, and are probably similar in the other two reservoirs. Spawning begins as early as the first week of April, generally peaks during the first week of May, and is essentially completed by the last week of May. The spawning sequence proceeds from the upper ends of tributaries downstream towards the dams. Water temperatures during spawning range from 8 to 13°C and peak spawning occurs at 10°C.

The incubation period of the eggs laid earliest usually lasts about 3 wk, but after water temperatures rise, the incubation period is reduced to 10–14 days. The young hatch from the first week of May to the first week in June. Although spawning and hatching are extended over a relatively long period, hatching at any single locality is generally completed within 2 wk.

Abundance and distribution — The relative abundance of young-of-the-year yellow perch was consistently lower in Lewis and Clark Lake than in the other three reservoirs (Fig. 2). In Lakes Oahe and Francis Case, their abundance increased rapidly as these reservoirs filled. After full pool was attained in Lake Oahe, abundance decreased greatly; in Lake Francis Case young perch were never as abundant as in Lake Oahe, but abundance did not consistently decline, and peak seine catches occurred 10 and 14 yr after the reservoir filled. The general trend in abundance of young perch in Lake Sharpe was similar to that in Lake Oahe; abundance gradually declined from the third to sixth year of impoundment but then increased.

Abundance of adult yellow perch was lowest in Lewis and Clark Lake and highest in Lake Francis Case (Fig. 3). The adult stock reached a maximum during filling of Lake Oahe but declined greatly after the reservoir was filled, and remained relatively low through the early 1970s. The population in Lake Sharpe also increased during the first years of impoundment and then stabilized at a low level.

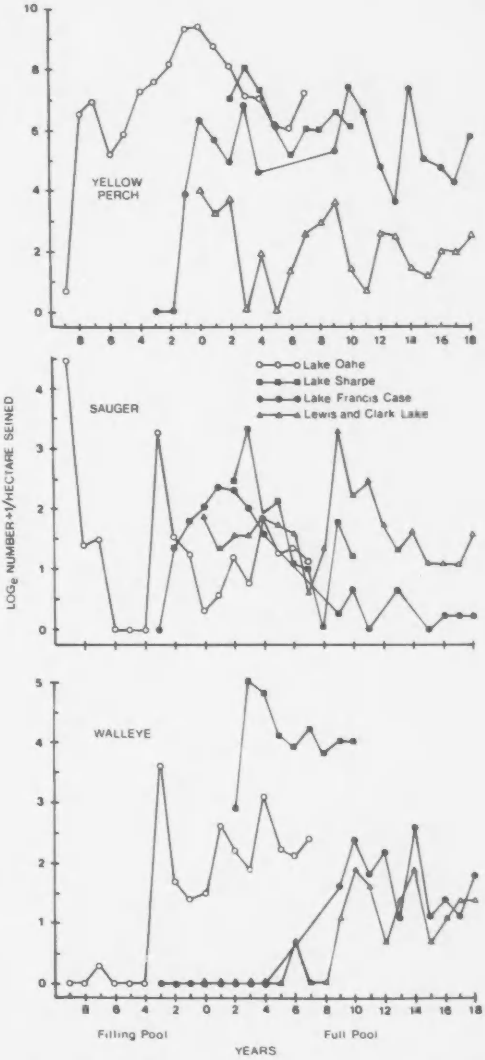

FIG. 2. Mean numbers of young-of-the-year of three species captured per hectare seined during the years before and after the reservoirs filled.

Seine catches of young yellow perch were generally highest in the shallow more productive areas of the reservoirs. Less than 5% of the young taken in Lewis and Clark Lake in 1965–73 were collected in the turbid, riverlike upper half, and in Lake Francis Case the riverlike upper third contributed only 18%, and in Lake Sharpe only 16%. In Lake Oahe catches declined with time in the deeper and less productive lower section from 57 to 17% of the total.

Growth — First-year growth of yellow perch varied little in Lakes Francis Case, Sharpe, and Oahe (Fig. 4). Mean length varied among reservoirs by only 6 mm during the first week in July

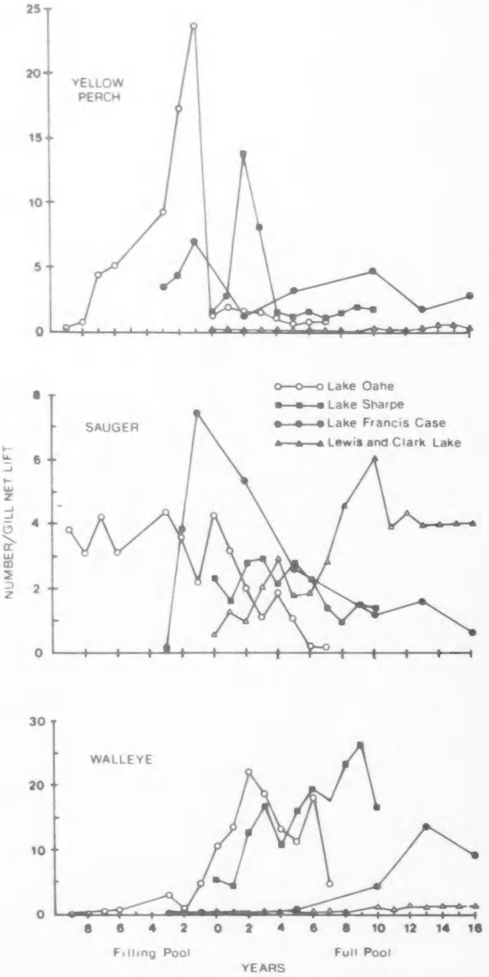

FIG. 3. Mean numbers of adults of three species captured per gillnet lift during the years before and after the reservoirs filled.

and by only 1 mm by the third week in August. First-year growth increased steadily from 54 mm in 1967 to 67 mm in 1974 in Lake Sharpe and from 62 to 79 mm during the same years in Lake Oahe. First-year growth in Lake Francis Case fluctuated between 62 and 71 mm in different years without trend.

After three growing seasons, yellow perch had attained a greater mean length in Lake Francis Case than in Lakes Sharpe or Oahe (Table 3); however, differences in mean lengths between year-classes in a reservoir were greater than the differences among reservoirs. After 3 yr of growth, the maximum differences in mean lengths between year-classes were 52, 40. and 28 mm in Lakes Francis Case, Sharpe, and Oahe, respectively. In general, growth was most rapid during the early years of impoundment, declined, and then improved slightly.

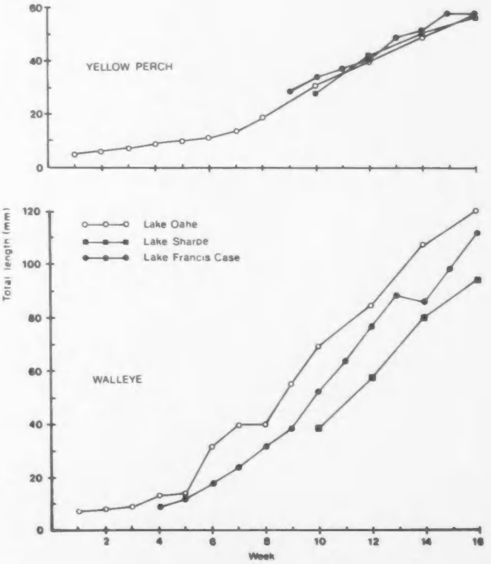

FIG. 4. First-year growth of yellow perch and walleyes from May through August.

In Lake Oahe, there was a significant difference (Student's *t*-test) in length attained in different sections of the reservoir as well as differences with time. Mean lengths (mm) of female yellow perch (sexes combined for 1-yr olds) captured in 1969 and 1974 in the lower and upper sections of Lake Oahe were:

Years of growth	1969 Lower		1969 Upper
1	71.5	$P < 0.01$	63.1
2	118.3	$P < 0.01$	127.6
3	159.3	$P < 0.01$	170.7
4	185.0	$P > 0.10$	187.1

Years of growth	1974 Lower		1974 Upper
1	74.6	$P < 0.01$	70.4
2	150.6	$P < 0.01$	141.6
3	176.6	$P < 0.05$	160.3
4	197.0	$P < 0.05$	180.2

Yellow perch that had completed two or more growing seasons when they were captured in 1969 had attained greater lengths in the upper sections

TABLE 3. Unweighted mean total lengths (mm) of three species at end of each year of life in Missouri River reservoirs.

		Lengths at end of year								
Reservoir		1	2	3	4	5	6	7	8	9
Yellow perch										
Francis Case	Mean	69	142	187	211	—	—	—	—	—
Sharpe	Male	—	146	155	179	193	—	—	—	—
	Female	—	152	170	187	204	—	—	—	—
	Mean	62	149	167	184	200	—	—	—	—
Oahe	Male	—	128	158	179	201	213	—	—	—
	Female	—	134	167	191	207	224	—	—	—
	Mean	69	132	165	189	206	219	—	—	—
Sauger										
Lewis & Clark	Mean	146	257	327	386	436	492	541	576	—
Francis Case	Mean	140	265	344	418	478	518	570	—	—
Sharpe	Male	—	285	344	368	405	464	502	—	—
	Female	—	252	334	428	468	528	541	—	—
	Mean	—	269	339	389	444	517	533	—	—
Oahe	Male	—	267	323	382	425	477	508	—	—
	Female	—	255	329	407	465	526	532	—	—
	Mean	140	260	327	399	455	521	522	—	—
Walleye										
Lewis & Clark	Mean	167	273	356	421	480	547	584	640	—
Francis Case	Mean	130	274	374	417	480	540	579	599	621
Sharpe	Male	—	259	350	400	447	483	514	528	560
	Female	—	257	341	424	503	542	606	623	677
	Mean	140	258	346	409	469	512	562	599	654
Oahe	Male	—	284	348	393	427	454	500	558	584
	Female	—	285	349	405	455	477	517	576	627
	Mean	163	285	349	399	439	474	513	569	617

than in the lower section. By 1974 the situation was reversed and the greater lengths were attained in the lower portion; however, except for 3- and 4-yr olds captured in the upper section, all lengths in both locations were greater in 1974 than in 1969.

Growth of yellow perch during their first summer in Lakes Sharpe and Oahe was inversely correlated with their abundance. In Lake Sharpe the correlation was not as high ($r = -0.64$; $P < 0.10$) as in Lake Oahe ($r = -0.87$; $P < 0.01$). Correlations between environmental characteristics and growth of adult perch were not significant.

Factors affecting year-class strength — The primary factors affecting year-class strength of yellow perch in Lakes Francis Case and Oahe were spring water levels and the amount of terrestrial vegetation inundated during the spawning period. In Lake Francis Case, year-class strength from 1966 to 1975, estimated by the number of young-of-the-year captured per hectare seined, fluctuated between 37 in 1970 and 1533 in 1967. Water level fluctuations during spawning ranged from a decrease of 1.5 m in 1970 to an increase of 3.8 m in 1967. Correlation of year-class strengths with changes in water level was significant ($r = 0.80$; $P < 0.01$).

Multiple regression analysis showed that two factors — the amount of newly inundated terrestrial vegetation and the change in water levels during spawning — accounted for 79% of the fluctuation in strength of year-classes established in Lake Oahe from 1968 to 1975 ($F = 9.64$; $P < 0.05$); the amount of newly flooded vegetation was the more important factor (0.97 relative importance). Abundance of young perch was not significantly correlated with the abundance of the primary predators, adult walleyes and saugers.

Survival — Meaningful survival rates for yellow perch were not determined from gillnet catches because of the late age of maximum recruitment. Fall catches with 10.7-m bottom trawl in Lake Oahe in 1965–74 gave the most reliable estimates. Unweighted mean survival rates from 1 to 6 yr of life were 30% for males, 49% for females, and 46% for the sexes combined. Survival was lowest from the first to second year (13%), and highest from the fourth to fifth year (85%).

Sauger

Reproduction — Nelson (1968b, 1969) found that little or no reproduction occurred in Lewis and Clark Lake; the major spawning ground was 11.3 km below Fort Randall Dam over a gravel, rubble, and boulder substrate. Sauger spawned in late April or early May when water temperature was about 6°C; peak activity lasted from 5 to 7 days and was completed in about 2 wk.

Abundance and distribution — Young saugers were most abundant in the years when the reservoirs were filling and in the first few years of full pool (Fig. 2). They were most common in Lewis and Clark Lake and least common in Lake Francis Case.

Catches of adult saugers in gill nets (Fig. 3) suggest that the Lewis and Clark Lake population increased from a low in the first year of impoundment to a high in the 10th year and thereafter stabilized at a slightly lower level. Relative abundances of saugers in Lakes Francis Case and Oahe were highest in the years before the reservoirs were full, and thereafter declined to a relatively low level. In Lake Sharpe the fish were most abundant during the first 6 yr after filling and then declined.

Distributions of young and adult saugers were similar in the four reservoirs; the fish were generally most abundant in the more riverlike, turbid, upper sections. The single exception was in Lake Sharpe, where young were most abundant in the middle section rather than the tailwater of Oahe Dam.

Growth — Comparison of average lengths of saugers at the end of each year of life in the various reservoirs suggests that growth was fastest in Lake Francis Case, intermediate in Lakes Oahe and Sharpe and slowest in Lewis and Clark Lake (Table 3). Growth rate of females was more rapid than that of males after the third or fourth growing season. Growth was greatest during early years of impoundment and declined somewhat in later years (Fig. 5).

Factors affecting year-class strength — Nelson (1968b) showed that fluctuations in abundance of the 1956–65 year-classes of Lewis and Clark Lake saugers were closely associated with hydroelectric power peaking operations at Fort Randall Dam. The difference in amounts of water released during the day and night caused fluctuations in water level over the downstream spawning ground that exposed incubating eggs to the air. Wallburg (1972) showed that more than 80% of the variation in year-class strength of Lewis and Clark Lake saugers could be explained by water level changes over the spawning ground, and mean June reservoir water temperature and exchange rate.

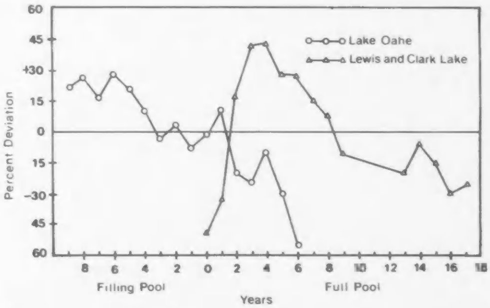

FIG. 5. Percentage deviation in mean annual growth of saugers during the years before and after Lakes Oahe and Lewis and Clark filled.

Survival — Annual survival rates by age were estimated for saugers captured in Lakes Lewis and Clark, Sharpe, and Oahe during various years. The unweighted means among age groups were variable, but the mean rate over ages II–VII was 0.55 (Table 4). Generally, survival rate decreased with age.

Walleye

Reproduction — Walleyes have exhibited adaptability in their reproductive habits in the reservoirs; spawning occurs in the original Missouri River, along reservoir shorelines, and in tributary streams. It usually occurs between early April and mid-May and, in any single year or impoundment, is usually completed within 7 to 10 days.

In Lewis and Clark Lake, which has no rubble shorelines, the only known spawning location is the previously described sauger spawning area in the Missouri River. However, walleyes usually spawned 7 to 10 days later than saugers. The presence of ripe male walleyes in the area when saugers were spawning and of ripe sauger males when walleyes were spawning led to occasional hybridization.

In Lakes Francis Case and Sharpe, walleyes spawn over boulder and rubble shorelines. Development of this substrate differed in the two reservoirs. Lake Sharpe was filled in 1 yr, and

TABLE 4. Unweighted mean survival rates by age-groups of saugers and walleyes captured with gill nets in three of the reservoirs.

Age-group	Lewis & Clark[a] Total	Sharpe[b]			Oahe[c]		
		Male	Female	Total	Male	Female	Total
			Sauger				
II–III	0.560			0.869			0.843
III–IV	0.654			0.978			0.685
IV–V	0.477			0.450			0.506
V–VI	0.721			0.450			0.389
VI–VII	0.337			0.144			0.132
Mean	0.550			0.578			0.511
			Walleye				
II–III	0.848	—	—	—	—	—	—
III–IV	0.566	0.644	0.731	0.680	0.538	0.775	0.752
IV–V	0.484	0.792	0.535	0.554	0.576	0.807	0.646
V–VI	0.791	0.381	0.480	0.469	0.440	0.532	0.468
VI–VII	0.333	0.459	0.420	0.527	0.351	0.834	0.691
VII–VIII	0.050	0.382	0.311	0.369	0.250	0.409	0.353
VIII–IX	—	0.400	0.667	0.545	0.444	0.444	0.444
Mean	0.512	0.510	0.524	0.524	0.443	0.617	0.559

[a] Sampled 1966–72.

[b] Sampled 1965–74 for walleyes and 1965–70 for saugers.

[c] Sampled 1965–73 for walleyes and 1959–62, 1965–76, and 1971–73 for saugers.

outcroppings of glacial till were immediately exposed. Lake Francis Case required 4 yrs to fill and rubble and boulders were not exposed until finer soils were gradually removed by wave action and fluctuating water levels.

Shoreline substrate for walleye spawning developed in Lake Oahe in the same manner as in Lake Francis Case; however, no evidence was found by 1975 that these shorelines were being used for spawning. Walleye eggs and larvae have been collected only in the three major tributaries — the Cheyenne, Moreau, and Grand rivers. These rivers are shallow and highly turbid, but flows are adequate to keep the soil particles in suspension and scour the bottom, and thus provide sufficient substrate for egg deposition. Because these streams warm rapidly in the spring, walleyes usually spawn from early to mid-April.

Abundance and distribution — Relative abundance of walleyes during their first year of life and as adults has been highest in Lake Sharpe and lowest in Lewis and Clark Lake (Fig. 2 and 3). In each of Lakes Oahe, Francis Case, and Lewis and Clark, only a single young-of-the-year walleye was seined during the first 6 yr after impoundment. Abundance was not determined during the first 3 yr of impoundment of Lake Sharpe, but thereafter the fish were more abundant than in the other reservoirs.

Large walleye populations have not developed in Lewis and Clark Lake, but after about 15 yr of impoundment a substantial population had developed in Lake Francis Case (Fig. 3). The walleye population developed more rapidly in Lake Oahe; adults were abundant within 10 yr after impoundment. The population in Lake Sharpe developed rapidly; adults became abundant within 4 yr after impoundment.

In Lakes Francis Case and Sharpe, relative abundance of young walleyes was highest in the central sections and lowest in the upper sections. About 60% of the catch in both reservoirs was taken in the central sections; the upper sections contributed about 19% in Lake Francis Case and 14% in Lake Sharpe. In Lake Oahe catches were also highest in the central section (41%) but the lowest catches occurred in the lower section (28%).

The distribution of adults varied among reservoirs. In Lewis and Clark Lake, 66% of the adult walleyes were caught in the lower half of the reservoir; in Lake Oahe, over 50% in the central third; in Lake Francis Case, about 43% from the upper third; in Lake Sharpe, during 1969–74, 36% in the lower section, 24% in the middle and upper sections, and 16% in the tailwaters of Oahe Dam.

Growth — The difference in length attained during the first year of life by walleyes in different reservoirs was apparently a function of spawning time rather than growth rate (Fig. 4). Walleye eggs generally hatched during the first week of May in Lake Oahe, as compared with the last week in May in Lake Francis Case and probably early June in Lake Sharpe. By the first week in July, the length of young averaged 38 mm in Lake Sharpe, 52 mm in Lake Francis Case, and 69 mm in Lake Oahe. Rates of growth after the first week in July were similar in all three reservoirs, but the walleyes in Lake Oahe maintained the advantage gained from early hatching and attained the greatest length.

Lengths attained by walleyes were greater in Lake Oahe than in the other three reservoirs during the first 2 yr of life, but thereafter lengths attained were greater in Lewis and Clark Lake and Lake Francis Case (Table 3). Growth of males and females varied little during the first three growing seasons in Lakes Sharpe and Oahe, but thereafter females grew faster than males.

Annual growth in Lewis and Clark Lake was relatively consistent, although the small sample sizes make interpretation difficult. In Lake Francis Case, lengths attained showed a marked decline after the early years of impoundment, but growth of individual year-classes was not followed closely because sampling was not done anually. In 1956, age II walleyes averaged 325 mm in length, but by 1973 they averaged 231 mm. From 1965 to 1973, the decrease in length ranged from 77 mm for age IV fish to 29 mm for age VIII fish.

Growth in Lake Oahe also declined markedly. After two summers, fish of the 1965 year-class averaged 327 mm in length and those of the 1973 year-class 221 mm; after five growing seasons the 1965 year-class averaged 472 mm and those of the 1970 year-class 397 mm. This apparent decline was primarily associated with the slower growth of fish captured in the lower third of the reservoir.

The mean lengths of female walleyes of the 1965–74 year classes captured in the lower, middle, and upper sections of Lake Oahe were:

	Lengths (mm) at end of year						
Section	1	2	3	4	5	6	7
Lower	156	228	292	349	387	426	477
Middle	165	279	349	416	476	511	541
Upper	152	281	355	433	475	506	567

After 2 yr, females were about 50 mm shorter in the lower third of the reservoir than elsewhere and after 5 yr the difference was nearly 90 mm. First-year growth varied little among sections of the reservoir or at any age in the upper two areas.

In Lake Sharpe, walleye growth declined after impoundment until 1970 and then stabilized or increased slightly. After 2 yr, fish of the 1964 year-class averaged 282 mm in length and those of the 1970 year-class 235 mm, but the 1973 year-class averaged 258 mm in length. Average length after 3 yr of growth declined from 374 mm for the fish of the 1964 year-class to 293 mm for fish of the 1970 year-class, but then increased to 317 mm for fish of the 1972 year-class.

Factors affecting year-class strength — Walleye year-class strength in Lake Oahe has been erratic, with nearly 30-fold differences among year-classes. The mean April flow rates in the tributaries in which walleyes spawned varied between 3.4 and 48.5 m^3/s annually. Multiple regression analysis of mean tributary flows, changes in mean flows, and air temperatures accounted for 55% of the variation of adult walleye year-class strength in 1965–74. Mean flows accounted for 70% of that variation. Temperatures were slightly more important than whether the flows were increasing or decreasing, but these factors were only about one-fifth as important as the mean flow. Relative abundance of yellow perch, other forage species, and adult walleyes were apparently unrelated to year-class strength.

In Lake Sharpe, where walleye spawn along shorelines, the factors affecting year-class strength differed from those in Lake Oahe. The independent variables of May wind velocity, air temperature, and forage fish abundance accounted for 89% of the variation in the abundance of young walleyes from 1967 to 1974. Abundance of forage fish accounted for about 91% of this total, with wind velocity negatively related and the second most important variable (−23%). Possibly the high degree of importance attributed to forage fish indicates that conditions favorable for walleye reproduction were also favorable for forage fish reproduction; however, it seems doubtful that the same environmental conditions could affect the reproductive success of species with such diverse spawning times and habits as walleyes and the main components of the forage fish population — yellow perch, gizzard shad, and emerald shiners. Inasmuch as walleyes have been observed by us to feed on their own young, it is possible in years when the forage fish population is low for walleyes to eat more of their own young and thus reduce their abundance. Chevalier (1973) reported that cannibalism may be a significant factor in determining year-class strength of walleyes in Oneida Lake.

In Lake Francis Case a similar situation exists since the abundance of young-of-the-year walleyes and yellow perch were strongly correlated

($r = 0.85$; $P < 0.01$). Abundance of young perch was attributed to high May–June water levels, but water levels were not highly correlated with walleye abundance ($r = 0.62$; $P < 0.10$). As in Lake Sharpe, the abundance of young walleyes was apparently dependent on abundant prey to provide food and reduce cannibalism. Forney (1974) found that the abundance of young yellow perch indirectly controls the size of the walleye populations in Oneida Lake by regulating cannibalism.

Survival — Walleyes were fully recruited to gill nets at age II in Lewis and Clark Lake and age III in Lakes Sharpe and Oahe. Mean survival rates from ages III to VIII ranged from about 44% in Lewis and Clark Lake to about 58% in Lake Oahe (Table 4). Females in both Lakes Sharpe and Oahe exhibited higher survival rates than did males, although in Lake Sharpe the difference between sexes was negligible.

Harvest

Percids have consistently been the most sought after species by anglers on Missouri River impoundments. Closure of Fort Randall Dam led to the development of an excellent sport fishery in 1954, with saugers — then an unregulated species — dominating the catch of more than 60,000 fish (Table 5). In 1955, after a daily limit of six saugers or walleyes per fisherman had been established, about 10,000 more saugers were harvested than in the previous year. Shields (1956) estimated that the sauger catch would have been about 23,000 higher if the previous no-limit regulation had still been in force. Even though the sauger–walleye limit was liberalized to 10 per day in 1956, the catch declined about 60% from 1955. Shields (1957b) attributed this decline to unfavorable weather, but since the catch remained at this level in 1957–58, it appears probable that the closure of Gavins Point Dam (111 km downstream) in 1955 was a contributing factor because it blocked upstream migration.

Although the sport fishery in the tailwaters of Lake Francis Case was primarily for saugers, crappies constituted a substantial portion of the catch in 1955. Yellow perch harvest increased from 1954 to 1956 (Shields 1957b) but then began to decline. Walleyes constituted less than 1% of the total harvest until 1958, when they made up more than 3% (Sprague 1959). The legalization of paddlefish snagging in 1957 resulted in a substantial increase in the weight of sport fish harvested (Shields 1958).

After Lake Francis Case began filling, sportfishing effort increased and success decreased annually (Table 5). After 7 yr of impoundment the harvest was only 1.35 kg/ha, although effort exceeded 13 h/ha. Initially, the fishery was chiefly for black bullheads, largemouth bass, crappies, and yellow perch, but by 1960 these species contributed little to the catch, and saugers accounted for nearly 25% (Nelson 1961). During these years few walleyes were caught, but their importance was increasing.

Fishing effort in the tailwaters of Oahe Dam (Table 6) was considerably higher than had been recorded in the tailwaters of Lake Francis Case (Fogle 1961a, b, 1963a, b; Schmidt 1975). Total catch per hour was lower in Oahe tailwaters than in the Francis Case tailwaters, although sauger catches were similar.

During the first 3 yr of creel census in the Oahe Dam tailwaters, saugers accounted for about 50% of the total catch by number, and walleyes increased from about 4% in the first year to 8%. By 1973–74, contributions by these species had reversed; walleyes accounted for about 76% of the catch and saugers for 4%. The predominance of walleyes was more pronounced in Lake Sharpe, where they accounted for 89% of the total catch; saugers contributed less than 2%. Walleye catches in Lake Sharpe and the contiguous Oahe tailwaters accounted for 0.29 fish/h and 1.55 kg/ha of the 0.34 total fish/h and 1.96 kg/ha harvested (Schmidt 1975). Yellow perch were not an important part of the harvest.

Status of the Percid Stocks

After the reservoirs filled, percids increased in relative abundance while other groups of fishes declined. In Lake Oahe percids constituted about 5% by weight of the gillnet catches in 1960 (Fogle 1961b), but from 1971 to 1973 they averaged nearly 22%. During these same years species such as carp, bigmouth buffalo, and smallmouth buffalo declined significantly (Gabel 1974; Nelson and Boussu 1974). Walburg (1976) showed that in Lewis and Clark Lake the contribution of sport species increased from 14 to 24% of the estimated biomass between 1966 and 1972, and percids were the only sport species that had increased in abundance. During the same years, nonsport species declined 69%. Thus, the primary cause for the increased relative composition of percids was the decline in total biomass.

Abundance of perch was low in the original Missouri River, but as the reservoirs filled ideal spawning conditions were created, and strong year-classes were produced (Beckman and Elrod 1971; Gasaway 1970). After the reservoirs filled,

TABLE 5. Sport fishing effort and harvest of saugers, walleyes, yellow perch, and all species combined, Lake Francis Case[a] and its tailwaters, 1954–60 (From Shields 1955, 1956, 1957b, 1958; Sprague 1959; Nelson 1961).

	Lake Francis Case tailwaters					Lake Francis Case			
Item	May 1954–Mar. 1955	Apr. 1955–Mar. 1956	Apr. 1956–Mar. 1957	Apr. 1957–Mar. 1958	Apr. 1958–Mar. 1959	May 1954–Nov. 1954	Apr. 1955–Dec. 1955	Apr. 1956–Dec. 1956	May 1960–Sept. 1960
Effort (h)	91,700	167,900	108,080	98,824	72,000	84,010	119,264	158,849	425,000
Sauger									
Number	26,876	36,351	14,735	15,930	14,215	230	594	1,043	28,821
Weight	15,243	19,792	10,924	12,407	11,353	25	108	378	12,684
No./h	0.29	0.22	0.14	0.16	0.20	—[b]	0.01	0.01	0.07
kg/ha	188.20	244.30	134.90	153.20	140.20	—[c]	—[c]	0.01	0.36
Walleye									
Number	484	743	360	91	1,323	0	190	177	1,386
Weight	275	506	317	69	1,284	—	34	116	1,735
No./h	0.01	—[b]	—[b]	—[b]	0.02	—	—[b]	—[b]	—[b]
kg/ha	3.40	6.2	3.90	0.90	15.90	—	—[c]	—[c]	0.05
Yellow perch									
Number	1,211	8,024	15,946	10,514	3,102	25,460	9,361	21,039	3,793
Weight	84	910	1,305	1,040	397	1,760	849	2,218	241
No./h	0.01	0.05	0.15	0.11	0.04	0.30	0.08	0.13	0.01
kg/ha	1.00	11.20	16.10	12.80	4.90	0.09	0.03	0.08	0.01
All species									
Number	60,532	126,440	73,803	66,496	38,123	114,910	105,216	89,421	114,310
Weight	25,986	38,689	26,599	54,551	17,297	14,242	16,323	18,093	48,176
No./h	0.66	0.75	0.68	0.67	0.53	1.37	0.88	0.56	0.27
kg/ha	320.80	477.60	328.40	673.50	213.50	0.70	0.58	0.64	1.35

[a] Dam closed in 1952 and impoundment reached base of flood control in 1957.
[b] Less than 0.005 fish/h.
[c] Less than 0.05 kg/hectare.

TABLE 6. Sportfishing effort and harvest of saugers, walleyes, yellow perch, and all species combined from Lake Sharpe[a] and the tailwaters of Lake Oahe[b], 1960–63 and 1973–74 (From Fogle 1961a, b, 1963a, b; Schmidt 1975).

	Lake Oahe tailwaters				Lake Sharpe
Item	June 1960–May 1961	June 1961–May 1962	June 1962–May 1963	June 1973–May 1974	June 1973–May 1974
Effort (h)	241,029	212,521	131,123	72,715	170,874
Sauger					
Number	58,508	44,129	27,085	529	1,222
Weight	44,814	40,297	17,733	368	665
No./h	0.24	0.21	0.21	0.01	0.01
kg/ha	553.3	497.5	218.9	0.6	—[d]
Walleye					
Number	4,752	5,553	3,782	11,599	59,317
Weight	6,991	3,225	4,617	8,621	26,883
No./h	0.02	0.03	0.03	0.16	0.35
kg/ha	86.3	39.8	57.0	15.1	1.2
Yellow perch					
Number	11	332	198	9	856
Weight	1	21	10	1	108
No./h	—[c]	—[c]	—[c]	—[c]	0.01
kg/ha	—[d]	0.3	0.1	—[d]	—[d]
All species					
Number	128,189	97,388	46,288	15,302	66,317
Weight	171,076	166,400	42,009	11,063	33,843
No./h	0.54	0.46	0.35	0.21	0.39
kg/ha	2,112.0	2,054.3	518.6	19.4	1.5

[a] Dam closed in 1963 and impoundment reached base of flood control in 1965.

[b] Dam closed in 1958 and impoundment reached base of flood control in 1967.

[c] Less than 0.005 fish/h.

[d] Less than 0.05 kg/ha.

spawning habitat deteriorated, and strong year-classes were produced only in years of high water. By the mid-1970s yellow perch were most abundant in sections of the reservoirs that tended to be shallow and productive and least abundant in those that tended to be deep and less productive or riverlike.

The yellow perch is the primary prey of both walleyes and saugers, and apparently when its abundance declines to a low density these predators use other species, such as gizzard shad and white bass. This compensatory mortality has probably contributed to the relatively consistent abundance of adult yellow perch in recent years — a development which could be expected in the complex communities of these reservoirs (Ivlev 1961).

Saugers were the predominant percid in the original Missouri River. After impoundment the numbers increased, but after lakelike conditions had developed and spawning habitat was reduced, the populations declined to low levels in all reservoirs except Lewis and Clark Lake. By the mid-1970s, sauger populations were primarily associated with the upper sections of the reservoirs where the more turbid, flowing waters most closely approximated the original river habitat.

Walleyes were scarce in the river before impoundment. The population developed slowly in Lake Francis Case and was apparently dependent on the development of suitable spawning substrate of rubble and gravel. The Lake Sharpe population probably developed more rapidly because suitable spawning substrate was immediately available. Present walleye distribution in these reservoirs agrees well within the preferred habitat described by Regier et al. (1969). Peak abundance occurs in sections of intermediate water clarity and depth; walleyes are least abundant in highly turbid, flowing waters, such as Lewis and Clark Lake or the upper portions of the other impoundments, and in the clear, deep waters in the lower portion of Lake Oahe.

Recent estimates of walleye and sauger harvest were available only for Lake Sharpe and the tailwaters of Lake Oahe. Although catch rates were higher in Lake Sharpe, both fishing pressure and harvest were about half those reported for large walleye lakes in Minnesota (Johnson 1975). Because of its smaller size and better facilities for anglers, Lake Sharpe has heavier fishing pressure than do the other impoundments. Harvest ranges from moderate in Lake Sharpe to virtually nil elsewhere, and has not had a measureable effect on the populations in any of the reservoirs. However, estimated survival rates of walleyes in these reservoirs are lower than those reported from lakes where exploitation is greater (Forney 1967; Johnson 1975).

The future abundance of the yellow perch, sauger, and walleye populations appears to depend on reproductive success, since fishing pressure and cultural eutrophication are not expected to increase. Reproductive success will be governed largely by amount of precipitation, water levels, water exchange rate, and the rate of accumulation of silt from tributary inflows and bank sloughing. The expected long-term effect of these processes is a gradual degradation of the environment, which in turn will lead to a lower total productivity. However, we forsee no significant changes in the yellow perch, walleye, and sauger populations in the near future, unless a species such as the recently introduced rainbow smelt changes the ecological balance.

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Effects of Fisheries on Eurasian Perch (*Perca fluviatilis*) in Windermere[1]

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BAGENAL, T. B. 1977. Effects of fisheries on Eurasian perch (*Perca fluviatilis*) in Windermere. J. Fish. Res. Board Can. 34: 1764–1768.

A review of literature indicated that a wartime (1941–48) trap fishery reduced the Eurasian perch (*Perca fluviatilis*) population very considerably. An experimental gillnet fishery for northern pike (*Esox lucius*) from 1944 to 1975 presumably contributed to keeping the perch population low through increased predation. The gillnet fishery reduced the average size of the pike, and their growth rate increased, in turn increasing the predation on younger perch. This predation controlled recruitment to the adult perch population. Pike predation is given as one factor in a model explaining year-class fluctuations.

Key words: Percidae, exploitation, year-class fluctuations, *Perca* predation, year-class model

BAGENAL, T. B. 1977. Effects of fisheries on Eurasian perch (*Perca fluviatilis*) in Windermere. J. Fish. Res. Board Can. 34: 1764–1768.

Une revue de la littérature indique qu'une pêche au piège pendant la guerre (1941–48) réduisit considérablement la population de perches eurasiennes (*Perca fluviatilis*). Une pêche expérimentale de grands brochets (*Esox lucius*) au filet maillant entre 1944 et 1975 contribua probablement, par une prédation accrue, à maintenir la population de perches à un bas niveau. La pêche au filet maillant entraîna une diminution de la taille moyenne et une augmentation du rythme de croissance du grand brochet, intensifiant de cette façon la prédation sur les jeunes perches. Cette prédation exerça un contrôle sur le recrutement de la population de perches adultes. La prédation par le grand brochet est considérée comme un facteur dans un modèle expliquant les fluctuations des classes d'âge.

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THIS paper is a review of the effects on Eurasian perch (*Perca fluviatilis*) in Windermere of an intensive fishery during the 1939–45 war, followed by winter gill netting from 1944 to 1975 of northern pike (*Esox lucius*), which from 3 cm upwards is a major perch predator. Detailed accounts of these two fisheries were given by Bagenal (1970) and Le Cren et al. (1972).

History of Windermere and its Fish

Windermere, which lies in a valley of glacial origin, is 17.0 km long and is divided by a group of islands into two basins. The lake has been studied by the Freshwater Biological Association for many years and its history, physics, chemistry, and biology were summarized by Macan (1970). Pennington (1973) described the history determined from the sediments. Accounts of the commercial fisheries to their cessation in 1921 were given by Watson (1925) and Kipling (1972).

Besides the perch and pike, the commonest fish species are char (*Salvelinus alpinus*), studied by Frost (1946, 1965); trout (*Salmo trutta*), which has not been studied in detail since Allen (1938); the European eel (*Anguilla anguilla*), considered by Lowe (1952), and the minnow (*Phoxinus phoxinus*), studied by Frost (1943). Other species present are the salmon (*Salmo salar*), the bullhead (*Cottus gobio*), roach (*Rutilus rutilus*), and the three-spined stickleback (*Gasterosteus aculeatus*). The rudd (*Scardinius erythophthalmus*) and tench (*Tinca tinca*) are very rare.

The Association's Fishery Programs

In the wartime fishery from 1941 to 1947 over 90 t of perch were trapped and canned for human consumption. The background reasoning, the methods and the scientific aspects of the fishery, together with the effects during the first 8 yr, were described by Worthington (1950). Large scale removal of perch continued in the north basin until 1948 and in the south basin until 1964, after which traps were only set for monitoring and sampling for study. Traps were set for 6 wk from mid-April and lifted weekly, mainly from one sampling site in the north basin and three in the south. Each fish in the sampling

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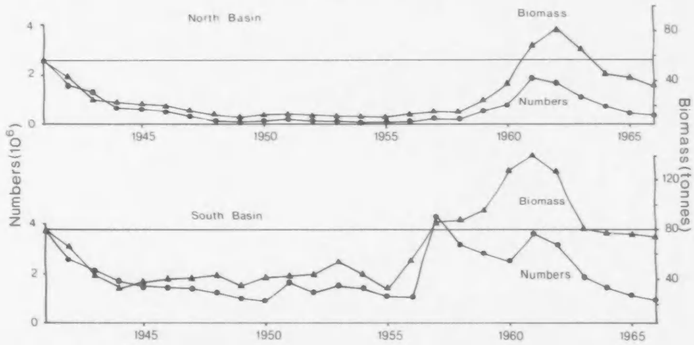

FIG. 1. Esitmated numbers and their biomasses of perch aged 2–18-yr-old in the North and South basins of Windermere from 1941 to 1966.

catches was measured and sexed and the opercular bone removed for age determination. Studies of the catches were published by Bagenal (1972), Kipling (1976), Le Cren (1947, 1955, 1958), Le Cren et al. (1972, 1977), and McCormack (1970).

In the fishery for northern pike, gill nets of 64 mm bar, first made of flax and later of terylene, have been used from the winter of 1944–45 to the present. These nets catch pike of 55 cm and over and, because the females grow faster than the males, they catch females of 3-yr-old and older and males of 4 yr and older. From 1944 to 1975, 11,591 pike, weighing 33.9 t, were removed from Windermere and measured, weighed, sexed, and aged, and the stomach contents noted. Each spring since 1949 nets have also been set to tag pike, and up to 1975 4,434 were tagged. Studies of the pike were published by Frost (1946, 1954), Frost and Kipling (1967), Kipling and Frost (1970), and Le Cren et al. (1972).

Effects of the Two Fisheries

The main effects of the wartime fishery were to reduce the number of perch in the lake (Fig. 1) and to alter the sex ratio and growth rate. The traps were set during the spawning season, when the catches are greatest (Craig 1975) and very selective for males, though for perch between 9 and 30 cm the traps do not appear to be size selective (Le Cren 1953). The mean annual growth increments of male perch from 1933 to 1950 increased from about 5 to 29 g (Le Cren 1958), but these could not be related closely to the increases in the population density.

Perch are important in the diet of pike of 3 cm upwards (Frost 1954). The main effects of the pike fishery that have affected perch have been changes in age distribution, growth rate, and numbers of pike. There are now considerably more younger pike in the catches relative to old pike than there used to be (Table 1) and, although the differences are not large, the pike tend to be heavier since 1952 than they were in 1944–45 (Table 2). After the initial decrease after the start of the gill netting, the number of pike up to 1968 did not drop below the 1944 level except in 1956 (Fig. 2). In 10 of the years the population was over 20% greater than before the fishing started. However, only in 1962 was

TABLE 1. Percentage distributions of three age-groups of gill net-caught male and female pike in the first year of fishing, 1944–45, and in three subsequent periods.

Age	1944–45		1952–55		1962–65		1972–75	
(yr)	♂	♀	♂	♀	♂	♀	♂	♀
<5	9.4	26.1	29.8	63.0	23.7	56.9	56.6	79.0
5–9	82.0	62.9	69.7	35.8	75.8	42.7	42.4	20.6
>9	8.6	11.0	0.5	1.2	0.5	0.4	1.0	0.4

TABLE 2. Mean weight (kg) of gillnetted male and female pike of three ages caught in the first year of fishing, 1944–45, and in three subsequent periods. The average % increase is the increase in the figures for the last two decades over 1944–45.

	Age 4		Age 7		Age 10	
Years	♂	♀	♂	♀	♂	♀
1944–45	1.81	2.65	2.79	5.73	3.49	8.15
1952–55	1.97	2.71	2.95	5.99	—	9.36
1962–65	1.86	2.51	2.64	5.41	4.03	—
1972–75	2.19	3.20	3.20	7.26	3.38	7.10
Average % increase	9.95	5.91	5.02	8.55	6.16	0.98

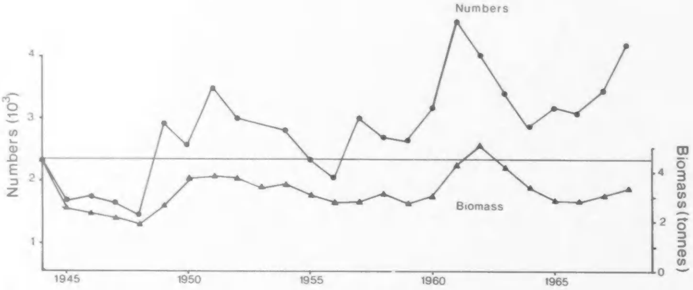

FIG. 2. Estimated numbers of adult pike and their biomasses in Windermere from 1944 to 1968.

the biomass greater than in 1944, and in that year it was high due to the successful 1959 year-class. This indicates that the population was made up of younger and lighter pike than before the netting started. Le Cren et al. (1972) hypothesized that the effects of the pike gill netting were to increase the predation on the perch. They pointed out that only in exceptional years was there much perch recruitment and that the failure of the perch to return permanently to the prewar numbers (Fig. 1) seemed to be due to higher and variable juvenile mortality. Since pike tend to eat perch of a quarter to a third of their own length (Table 3), and the frequency of perch in stomachs of small pike was often high (up to 83% (Frost 1954) for some length groups), the result of the pike gill netting was to increase the predation on the smaller perch.

Kipling and Frost (1970) estimated, for the 1951 pike year-class, that 63% of the total food consumption occurred during the first 2 yr of life. These fish would be up to about 40 cm in length (Frost and Kipling 1967). From Table 3, we see that pike up to this size tend to eat perch up to 9.3 cm mean length. The gillnets catch pike of 55 cm and larger and the fishery has increased the number of pike smaller than this. From Table 3, we see that pike of less than 55 cm tend to eat perch of less than 12.6 cm. Since the estimated weight of food consumed by pike shows no decreasing trend (table 15 in Kipling and Frost 1970) but varies due to year-class strength, it can be presumed that the number of young perch eaten has increased.

TABLE 3. Mean length of perch eaten by different sized pike (from Frost 1954).

Pike length group (cm)	Mean length of perch prey (cm)	Perch length as a percentage of perch length
20–29	6.1	25
30–39	9.3	31
40–49	10.3	26
50–59	12.6	25
60–69	12.8	20
70–79	13.7	20
80–99	13.1	14

Furthermore, McCormack (1970) found that although O group perch were not of great importance in the diet of larger perch, as found by Alm (1946) in Sweden, perch were cannibalized by those of 11.5–13.9 cm, whereas Allen (1935) only recorded perch in the diet of those longer than 16 cm. Furthermore, the increased growth rate means that perch become cannibals at a much younger age, so that total predation on young perch by perch may be much greater than it was.

The increased perch populations in the south basin in 1957 and 1961 (Fig. 1) were dominated by the very successful 1955 and 1959 year-classes. These years also produced strong pike year-classes so predation kept in step with the perch numbers; and since gill netting would not reduce pike until they were 3- or 4-yr-old, they were available for this length of time to prey on perch. By 1963 the perch population had again been reduced to the 1945 level. Those which survived the predation would be too large for the majority of the pike and indeed some of the 1955 year-class were caught in 1975.

The effect of the pike fishery in keeping the perch population low was probably effective only because the perch numbers had already been reduced. Before the intensive perch fishery the population consisted of many small slow-growing perch. An increased pike predation then would therefore have been spread over many age-groups. The effects on recruitment would have been less marked and the population less radically affected.

In spite of the increased predation, which Le

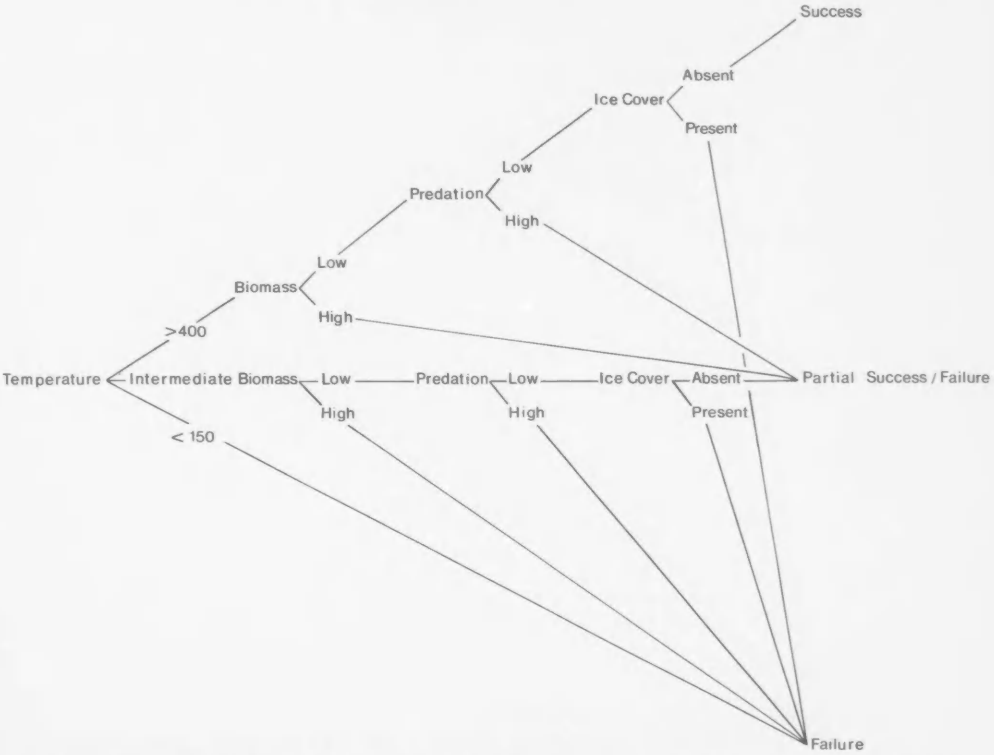

Fig. 3. Diagram of Kipling's (1976) hypothesis for determination of perch year-class strength in Windermere.

Cren et al. suggest largely controls recruitment to the adult population, recruitment varied very considerably from year to year. Predation is therefore only one factor affecting year-class strength. Kipling (1976) put forward a hypothesis (Fig. 3) to explain perch year-class differences which includes factors in addition to predation. These she correlated with year-class strength over a 24-yr period. The most important factor appeared to be temperature and she used Le Cren's (1958) temperature index, which was the cumulative total of the number of degrees that the daily surface water temperature readings were above 14°C. She showed that particularly successful year-class correlated with warm summers when the index was over 400, combined with low biomass of adult perch in the lake. Poor year-classes were associated with a variety of factors, any one of which might lead to partial failure. The factors consisted of cold summers when the index was less than 150, a high adult perch biomass, heavy pike predation and ice cover the previous winter. The most important factor in the model is undoubtedly the weather, over which man has no control, but his activities could be made to affect year-classes through fisheries leading to changes in perch biomass and pike predation.

Postscript

Since this paper was written the Windermere perch have suffered very considerably from an infection of *Aeromonas* sp. During the autumn of 1976 it was impossible to catch adult perch using methods that would previously have caught hundreds. The extent of the mortalities will be assessed in future years. At present it appears that the depopulation (and there is no evidence that it is not a natural event) has had a greater affect than any of man's known activities recorded in this paper.

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Exploitation of Walleye (*Stizostedion vitreum vitreum*) in Lac Des Mille Lacs, Northern Ontario, by Commercial and Sport Fisheries, 1958–75[1]

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Elsey, C. A., and R. T. Thomson. 1977. Exploitation of walleye (*Stizostedion vitreum vitreum*) in Lac des Mille Lacs, northern Ontario, by commercial and sport fisheries, 1958–75. J. Fish. Res. Board Can. 34: 1769–1773.

Harvests by three types of gear from Lac des Mille Lacs showed considerable differences in size selection of walleye (*Stizostedion vitreum vitreum*). Angling gear was most selective for smaller walleye (primarily 4–6 years old) and commercial gill nets and trap nets were most selective for larger walleye (primarily 5–11 years old), indicating there was not effective competition for fish of the same size. The great difference in size selectivity of the gears should serve as a caution against basing inferences about the status of stocks based on harvest from a single or similar gear.

From 1971 to 1975 the total annual harvest (5.24 kg/ha) exceeded the theoretical potential yield (3.91 kg/ha) by 34%.

The large number of age-groups (1–12), the high sport fishery catch per unit of effort (0.40 fish per man-hour) and the lack of appreciable change in rate of growth suggested no inimical effects on the walleye fishery due to exploitation.

Walleye accounted for 62% of the total harvest (1971–75) reflecting both the preference for this species and their vulnerability to conventional (passive) commercial gear. The sport fishery harvest for the same period accounted for 92% of the total harvest.

Key words: Percidae, exploitation, *Stizostedion*, gear selectivity

Elsey, C. A., and R. T. Thomson. 1977. Exploitation of walleye (*Stizostedion vitreum vitreum*) in Lac des Mille Lacs, northern Ontario, by commercial and sport fisheries, 1958–75. J. Fish. Res. Board Can. 34: 1769–1773.

Les récoltes effectuées par trois types d'engins de pêche dans le lac des Mille Lacs accusent des différences considérables dans la sélection des tailles du doré jaune (*Stizostedion vitreum vitreum*). La pêche à la ligne exerce la plus grande sélection sur les dorés plus petits (surtout des dorés de 4–6 ans), et les filets maillants et filets trappes commerciaux sont les plus sélectifs des grands dorés jaunes (âgés surtout de 5–11 ans), ce qui indique qu'il n'y a pas de concurrence efficace pour des poissons de même taille. Cette grande différence dans la sélection des tailles par les engins devrait nous inciter à la prudence lorsqu'il s'agit de déterminer la condition des stocks en se fondant sur la récolte d'un seul engin ou d'engins semblables.

De 1971 à 1975, la récolte annuelle totale (5.24 kg/ha) dépassa le rendement possible théorique (3.91 kg/ha) de 34%.

Le grand nombre de goupes d'âge (1–12), les fortes prises par unité d'effort de pêche sportive (0.40 poisson par heure-homme) et l'absence de changement appréciable dans le rythme de croissance suggèrent que l'exploitation n'a pas d'effets nuisibles sur la pêcherie de dorés jaunes.

Le doré jaune constitue 62% de la récolte totale (1971–75), ce qui reflète la préférence dont jouit cette espèce et sa vulnérabilité aux engins conventionnels de pêche commerciale (passifs). Pour ce qui est de la pêche sportive, la récolte de dorés jaunes constituait pour la même période 92% de la récolte totale.

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Lac des Mille Lacs, approximately 70 miles northwest of the City of Thunder Bay in northwestern Ontario is a popular lake for walleye fishing. In this paper, we evaluate the various types of exploitation including size selectivity of the gear and their effects on the resource (1958–

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[2] Regional Fish and Wildlife Branch, North Central Region.

[3] District Fish and Wildlife Branch, Thunder Bay District.

TABLE 1. Physical and chemical (ppm) characteristics of Lac des Mille Lacs.

Surface area (ha)	24,000	Formazin turbidity units	4.2
Littoral zone (ha) (6.7 m)	13,900	Transparency (m)	1.6
Depth (m)		Apparent color	yellow-brown
maximum	24.4	Temperature	
mean	6.8	stratification	nil
Water fluctuations (m) (20-yr mean)	0.52	ph	
Volume, m^3	164×10^7	surface	6.8
Shoreline (km)		bottom (21.3 m)	6.0
lake	564	O_2	
islands	204	surface	8.2
development (Welch 1948)	10.3	bottom (21.3)	3.8
Basin shape	U	Nitrogen	
Bottom types (%)		free ammonia	0.02
clay	50	total kjeldahl	0.55
silt	20	nitrate	0.005
sand	10	nitrite	0.01
rock	10	Total phosphorus	0.011
detritus	10	Suspended solids	4
Flushing rate (yr) (20-yr mean)	4.5	Hardness ($CaCO_3$)	23
Morphoedaphic index (Ryder 1965)	3.04	Calcium	7
Conductivity		Magnesium	2
(corrected to 25°C)	48	Copper	0.010
TDS	68	Zinc	0.004
Alkalinity ($CaCO_3$)	18	Nickel	0.012

75). An analysis of catch per unit of effort and growth rates was undertaken to identify any trends resulting from exploitation. A comparison was made of the percentages of walleye in the sport and commercial fish harvests and the percentages of the sport fish harvest in the total harvest, to evaluate the relative importance of walleye to the two fisheries. Because of the high effort and yield and the possibility of overexploitation, the total harvest of all species was compared with the potential yield (Ryder 1965).

History of the Lake and Fisheries

Lac des Mille Lacs (Table 1) is a shallow, warm, brown-water lake on Precambrian bedrock. It has many bays, islands, inlets, and channels with a variety of depths, the maximum and mean being 24.4 and 6.8 m, respectively. Water levels are controlled by a 60-m cement dam on the Seine River which was constructed in 1953. The mean annual fluctuation for 1953 to 1975 was 0.54 m and the mean annual flow for the same period was 11.5 m^3/s. There were no obvious deleterious effects on the fisheries from water level fluctuations during 1961–75.

Fish species inhabiting the lake include walleye, northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), yellow perch (*Perca flavescens*), lake herring, cisco (*Coregonus artedii*), burbot (*Lota lota*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*). Walleye, northern pike, and lake whitefish were the only species of social and economic importance.

Species	Abundance	Commercial fishery	Sport fishery
Walleye	Abundant	Valuable	Valuable
Northern pike	Abundant	Less Value	Valuable
Lake whitefish	Common	Less Value	Incidental
Yellow perch	Common	Incidental	Incidental
Lake herring	Common	Incidental	Incidental
Burbot	Common	Incidental	Incidental
Suckers	Common	Incidental	Incidental

The first commercial tourist camp on the lake was built in 1946. There are now 12 catering to anglers. In addition, there is heavy fishing effort resulting from day users, campers, and 100 summer cottages.

Commercial fishing began in the lake in the early part of the 20th century and continued until 1921. It was resumed in 1944 and until 1950 there were six licenses on the lake; however, only two remained for the duration of this study.

Methods

The data for this report were obtained from three principal sources during a program to monitor the fish stocks. Commercial fishing reports during 1965 to 1975 supplied data on total catches but not on catches per unit of effort. Gill nets were used for walleye by both commercial fishermen until 1974, when one of the fishermen converted to trap nets. Creel censuses (Drysdale 1972, 1975) were conducted during 1958–75. During 1958–70 only catch per unit of effort data was collected and from 1971 to 1975 harvest data (kg/ha) were also collected. Experimental trap nets were set annually by the Ministry of Natural Resources to take a small number of walleye for monitoring purposes during 1965–75. In addition, while perhaps not typical, commercial trapnet data for 1975 was included. Fish scales were also collected.

Relations between the Fisheries

Selectivity of fishing gear — The age distributions of walleye in samples from the four fishing gears showed considerable variation (Fig. 1). Not all types of gear were necessarily used during the same years as described under methods. Most of the experimental trapnet catches ranged from age 4 to age 8, with age 5 predominant. Anglers were also most selective for age-5 walleye; however, the range was less, including primarily age-4 to age-6 walleye. While angling and experimental trap nets were declining in effectiveness for capturing age-6 and older walleye, commercial gill nets were only beginning to become effective, the catches ranging primarily from age 5 to age 10. At age 7, walleye were most vulnerable to commercial gill nets. The effectiveness of angling gear declined to a very low level and angling gear did not appear to catch walleye in proportion to their availability on the basis of the catches in the other gear. Commercial trapnet data for 1975 indicated the commercial fisherman was selectively fishing for very large walleye ranging primarily from age 8 to age 11, with age-10 fish predominant in the catch.

In the main, except for age-6 fish, the commercial fishermen and anglers were apparently not harvesting the same size or age of walleye, although big fish are important to anglers. Angling gear was most effective for smaller fish and commercial gear was selective for larger fish. The significance of the selectivity of angling gear for smaller fish is even more apparent if the percentage of very small fish, which were not included in the sample, are considered. Anglers returned a high percentage of their walleye catches to the lake due to their small size (39% in 1973, 24% in 1974, and 27% in 1975). Although the effects of recruitment were not taken into account, it appears that real competition between anglers and the commercial fishermen was primarily for kilograms and not for size of walleye.

Because selectivities for size of fish by the various types of gear differed markedly, it is important that managers do not attempt to base inferences about the status of stocks from a single sampling technique. Our experience suggests that creel census gave an impression of an exaggerated fishing-up process.

Trends resulting from exploitation — There was some reduction in angling success during 1958–75 (Fig. 2), with better success during 1958–68 (average 0.67 walleye per man-hour). This drop in catch per unit of effort was presumably a result of a fishing-up process and can be expected with even moderate levels of exploitation. There was no appreciable change in success rate from 1969 to 1975, and 0.40 walleye per man-hour compared favorably with the average success rate of 0.32 for walleye lakes in Minnesota (Hiner 1943; Colby et al. 1977). Because of this practically stable success rate, the annual variation in the walleye harvest during 1971 to 1975 appeared to be related to effort (Fig. 3) rather than density.

Although data on commercial fishing effort were not available, there was a general decline in catches from 1965 to 1971 for all three commercial species (Fig. 4), presumably in part because of reduced effort. Increased production after 1971 was primarily due to two factors. One fishery converted from a winter gill net to a fall trapnet fishery, resulting in a larger walleye catch; and the larger whitefish catch in 1974 and 1975 was due to addition of a summer gillnet permit for whitefish. As with the angling fishery, any recent

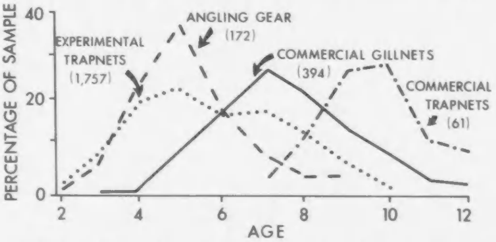

FIG. 1. Percentages of samples of walleye that were of various ages taken from experimental trap nets (1964–75) anglers catch (1971–75), commercial gill nets (1965–75), and commercial trap nets (1975). Numbers in parenthesis on figures are the number of fish in the sample.

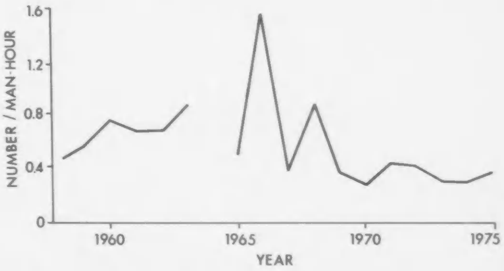

FIG. 2. Catches per unit of effort (number of fish per man-hour) of walleye in Lac des Mille Lacs, 1958–75 (as available).

TABLE 2. Mean fork lengths (cm) at ages 2–10 of walleye caught in experimental trap nets in Lac des Mille Lacs, 1965–75 (as available).

Year	Sample size	Age 2	3	4	5	6	7	8	9	10
1965	151	24.3	28.9	35.0	39.6	42.4	47.0	50.0	51.3	56.3
1969	296	24.3	28.4	34.0	38.8	43.2	47.7	52.0	51.8	
1971	298	26.1	32.5	36.3	40.9	41.4	47.4	53.8	57.1	63.2
1972	139	23.8	27.6	35.3	41.9	47.0	49.5	55.1		
1973	197		29.2	35.3	39.8	44.4	49.0	54.1	58.4	
1974	208	22.0	26.1	31.0	37.5	38.6	45.2	49.5	55.1	
1975	210	23.1	25.4	34.2	37.8	40.3	46.2	51.8	55.6	

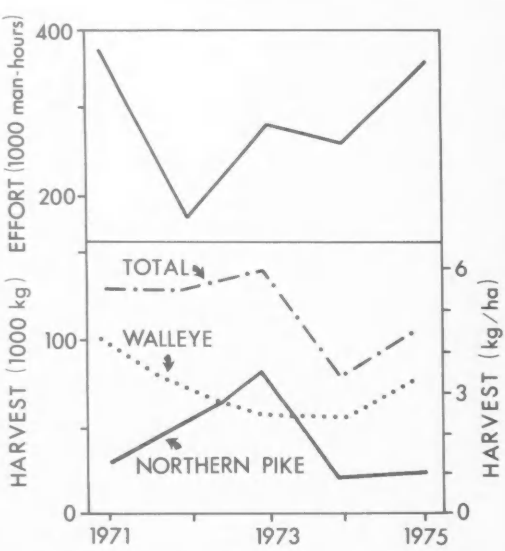

FIG. 3. Estimated weights of walleye, northern pike, and both species caught in the sport fishery (lower panel) and estimated fishing effort for walleye in man-hours (upper panel) in Lac des Mille Lacs, 1971–75.

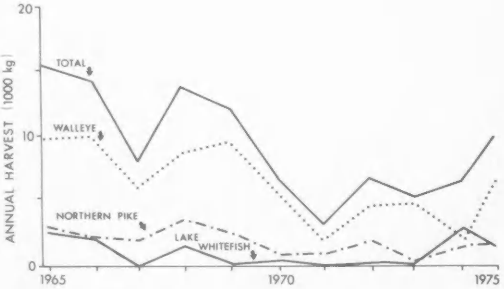

FIG. 4. Reported annual commercial harvests of walleye, lake whitefish, and northern pike and totals of all three species from Lac des Mille Lacs, 1965–75.

changes or trends in harvest appeared to be closely related to and resulting from changes in effort. The commercial harvest (Fig. 5) was apparently too small to affect the quality of the sport fishery materially by removing large numbers of larger fish.

Rates of growth for walleye remained practically constant during the experimental trap net sampling from 1965 to 1975 (Table 2). An exceptionally cold summer in 1974 probably slowed the rate of growth in that year. This was reflected in the age–length relationship in 1975. There was no evidence that the rate of growth was affected by exploitation.

Lac des Mille Lacs is a relatively heavily fished lake with a sport fishing effort of some 296,000 man-hours per year during 1971 to 1975 (Fig. 3). Walleye accounted for approximately 63% of the total sport harvest with northern pike accounting for the majority of the remainder of the catch during 1971–75 (Fig. 3).

Walleye was also the predominant species in the commercial fishery during 1965 to 1975 (Fig. 4). Both northern pike and lake whitefish

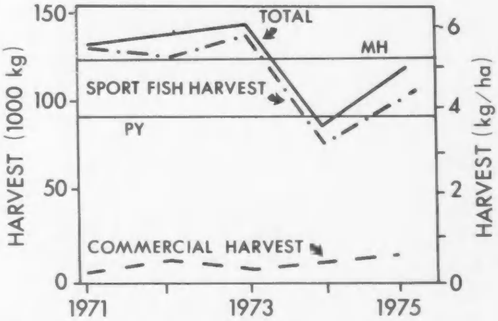

FIG. 5. Weights of the sport harvest, the commercial harvest and the total harvest in Lac des Mille Lacs, 1971–75. Parallel lines (kg/ha) indicate mean annual harvest (MH) and potential yield (PY).

catches were incidental to the fishery except in 1974 and 1975. Walleye accounted for approximately 55% of the total commercial harvest and 66% of the total marketable commercial harvest during 1971–75. These percentages were calculated for 1971–75 so they could be related to the sport fishery harvest for the same period.

Sixty-two percent of the total commercial and sport fish harvest was walleye. The sport fish harvest accounted for approximately 92% of the total harvest during 1971–75 (Fig. 5).

Potential yield vs. total harvest — The total annual harvest of the sport and commercial fisheries during 1971–75 (5.24 kg/ha) exceeded the calculated potential yield (Ryder 1965) of 3.91 kg/ha (Fig. 5). This indicated that the lake was being heavily fished and the fishery should be monitored closely for signs of overexploitation, i.e. changes in community structure, age structure, and age to maturity.

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Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*) Populations and Fisheries of the Red Lakes, Minnesota, 1930–75[1,2]

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SMITH, L. L. JR. 1977. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930–75. J. Fish. Res. Board Can. 34: 1774–1783.

In an investigation of the commercial fishery of Red Lakes, Minnesota, for the 46-yr period 1930–75, catch statistics were analyzed, and the dynamics of the perch and walleye populations were examined. Mean annual yields of walleye for two statistical periods, 1930–53 and 1954–75, were 309,900 and 245,100 kg, respectively for walleyes, and 96,400 and 109,500 kg for perch. Annual abundance (CPE based on average catches per day per 5-net units of gill nets) varied from 3.8 to 64.6 kg for walleye, and from 2.5 to 34.4 kg for perch. Causes of fluctuations in harvestable stock were directly related to strength of year-classes and to growth rate during the season of capture. Year-class strength was not related to the abundance of parent stock or of potential predators. The respective strengths of year-classes of perch and walleye in the same year were positively correlated ($r = 0.859$, $P < 0.01$), and are directly related to climatic factors. Growth rate of walleye in different calendar years varied from +30.7 to −42.2% of mean growth, and that of perch from + 13.4 to −8.6% (1941–56). Growing season began in mid-June and was almost over by September 1. Walleye yield could be enhanced by starting harvest July 1 instead of early June. Perch yield could be improved by harvesting small perch.

Key words: Percidae, *Perca*, population dynamics, *Stizostedion*, long-term yield

SMITH, L. L. JR. 1977. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930–75. J. Fish. Res. Board Can. 34: 1774–1783.

Lors d'une étude de la pêche commerciale dans les lacs Red, Minnesota, durant la période de 46 ans de 1930–75, nous avons analysé les statistiques de prises et examiné la dynamique des populations de perchaudes et de dorés jaunes. Les rendements annuels moyens en dorés jaunes pendant deux périodes statistiques, 1930–53 et 1954–75, furent de 309 900 et 245 100 kg respectivement pour le doré jaune, et de 96 400 et 109 500 kg pour la perchaude. L'abondance annuelle (fodée sur les prises moyennes par jour par unité de 5 filets maillants) variaient de 3.8 à 64.6 kg pour le doré jaune et de 2.5 à 34.4 kg pour la perchaude. Les causes des fluctuations dans le stock récoltable sont directement liées à l'abondance des classes d'âge et au rythme de croissance durant la saison de capture. L'abondance d'une classe d'âge n'a pas de relation avec l'abondance du stock parental ou des prédateurs possibles. L'abondance des classes d'âge de perchaudes est en corrélation positive ($r = 0.859$, $P < 0.01$) avec celle des dorés jaunes de la même année, et les deux sont en relation directe avec des facteurs climatiques. Le rythme de croissance du doré jaune pendant différentes années du calendrier varie de +30.7 à −42.2% de la croissance moyenne, et celui de la perchaude de + 13.4 à −8.6% (1941–56). La saison de croissance débute à la mi-juin et est presque terminée au 1^er^ septembre. On pourrait améliorer les rendements en dorés jaunes en commençant à les récolter le 1^er^ juillet plutôt qu'au début de juin. On pourrait également améliorer les rendements en perchaudes en récoltant les petites perchaudes.

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A commercial fishery that produced up to 727,300 kg (6.22 kg/ha) of fish in 1959 (average for 1930–75, 484,110 kg or 4.14 kg/ha) was conducted on the Red Lakes of northwestern Minnesota. Of the seven species taken, the walleye, *Stizostedion vitreum vitreum* and the yellow perch, *Perca flavescens* constituted the greatest

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Paper No. 9523, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minn. 55108, USA.

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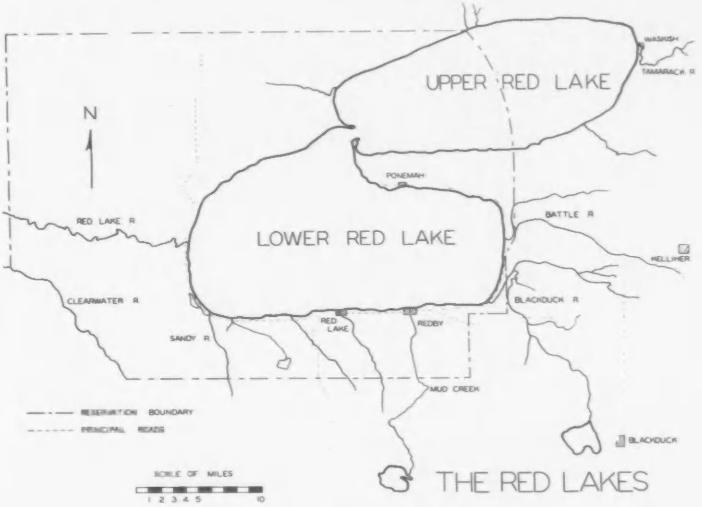

FIG. 1. Red Lakes, Minnesota.

portion of the production and revenue to the fishermen. Other commercial species were northern pike (*Esox lucius*), goldeye, (*Hiodon alosoides*), and freshwater drum, *Aplodinotus grunniens*. All commercial catches were taken by Indian residents of the Red Lakes Indian Reservation, within which lie the lower lake and two-thirds of the upper lake. Fish were taken exclusively in 8.9-cm mesh gill nets and processed through a cooperative fishery plant on the lower lake. Smith and Krefting (1953) showed that over a 24-yr period the amount of fishing effort did not influence the availability of fish or population size in later years. Smith et al. (1951) demonstrated through marking and recovery studies that walleyes in the upper and lower lake belong to the same population. No evidence of homing to spawning streams was noted. Smith and Pycha (1960) studied the development of Red Lake walleye during the first year of life. The early life history of the yellow perch was reported by Heyerdahl and Smith (1971). Ney and Smith (1975) described the life history of the yellow perch during the first year of life.

The present paper describes 46 yr of commercial fishery activity with special reference to walleye and yellow perch. It considers factors related to changes in fish abundance and describes characteristics of the population. The paper's objective is to examine fish production and the factors that influence it.

The two basins of the Red Lakes have a total area of 116,876 ha, a maximum depth of 10.7 m, and a mean depth of 5.5 m (Fig. 1). The lake has sandy shores, with a sand and gravel bottom extending to a depth of 2–3 m. The basins are remnants of glacial lake Agassiz and are abutted on the north and west by extensive bogs. Roughly oval in shape without embayments, the basins have a total shoreline length of 204.7 km. The index of shoreline development is 1.68. The lake is essentially isothermal, follows summer air temperatures closely, and is subjected to extreme wind-induced currents. The lake is moderately fertile; phosphorus and nitrogen concentrations have ranged from 0.08 to 0.085 and 1.6 to 2.0 mg/ℓ, respectively, and total dissolved solids from 160 to 221 mg/ℓ, depending on evaporation, extent of snow runoff, and rainfall. The morphoedaphic index and consequent theoretical yield (Ryder 1965) based on highest total dissolved solids is 40 and 5.7 kg/ha. Total alkalinity is 120–135 mg/ℓ as $CaCO_3$. Conductivity is 256–295 μmhos/cm.

Fishing is conducted from outboard-powered skiffs on days specified by the manager of the fishery cooperative. All fish are marketed through a cooperative operated by the Red Lake band of the Chippewa Tribe. The fishing season for percoids extends from June through early October; peak catches are in late July and early August. When lake whitefish (*Coregonus clupeaformis*) are available in harvestable quantities the season is extended into November. A sport fishery for walleye is carried on in the eastern half of the upper basin; conservation officers and the fishery

TABLE 1. Annual yield from Upper and Lower Red Lakes of perch, walleye, and all species 1930–75 in kilograms (thousands).

Year	All	Walleye	Cull walleye	Total walleye	Perch
1930	339.1	205.8	—	205.8	35.0
1931	482.1	338.8	—	338.8	43.6
1932	446.5	295.6	—	295.6	69.7
1933	355.7	245.1	—	246.1	83.1
1934	393.6	228.3	—	228.3	77.2
1935	327.5	163.1	—	163.1	76.2
1936	343.8	139.9	—	139.9	52.9
1937	462.3	278.8	—	278.8	107.9
1938	482.1	310.2	—	310.2	104.7
1939	430.2	263.1	—	263.1	90.8
1940	538.3	363.1	—	363.1	81.5
1941	553.3	422.0	—	422.0	44.8
1942	583.4	427.2	—	427.2	75.0
1943	595.6	356.3	17.7	374.0	92.5
1944	667.3	432.9	7.3	440.2	157.4
1945	658.9	389.0	7.2	396.2	146.5
1946	671.2	405.1	8.7	413.8	152.9
1947	696.4	427.4	16.3	443.7	152.5
1948	619.0	418.4	3.1	421.5	114.0
1949	481.5	288.6	11.1	299.4	84.2
1950	296.2	165.4	8.7	174.1	36.1
1951	343.9	247.4	5.1	252.5	50.8
1952	507.1	291.2	5.8	297.0	178.6
1953	478.7	234.8	9.2	244.0	206.0
1954	541.6	278.4	9.9	288.3	223.3
1955	523.4	283.0	9.8	292.8	155.9
1956	497.5	284.2	4.8	289.0	86.0
1957	520.6	297.0	5.6	302.6	97.6
1958	447.6	262.2	18.3	280.5	84.4
1959	727.3	181.2	60.6	241.8	137.4
1960	595.3	256.3	38.9	295.2	104.8
1961	435.2	300.3	2.6	302.9	74.4
1962	505.8	361.7	1.4	363.1	91.8
1963	501.1	201.0	8.7	209.7	140.5
1964	584.3	259.6	36.9	296.5	109.5
1965	610.3	193.0	63.0	256.0	199.8
1966	533.5	333.3	18.2	351.5	125.4
1967	420.2	286.6	5.6	292.2	92.8
1968	574.0	277.2	10.2	287.4	232.9
1969	586.8	283.5	10.4	293.9	203.4
1970	568.4	258.5	2.6	361.1	98.0
1971	469.0	205.7	16.2	221.9	59.5
1972	195.0	33.5	6.5	40.0	4.4
1973	140.0	28.3	0.6	28.9	4.4
1974	254.9	11.7	12.8	24.5	29.4
1975	283.6	71.7	0.8	72.5	54.0
1930–53 Means	489.7	305.7	9.1[a]	309.9[a]	96.4
1954–75 Means	478.0	229.4	15.6	245.1	109.5

[a] Includes walleye cull from 1943 to 1953 only.

manager estimate that the total catch by sport fishermen does not exceed 15–20% of the average commercial catch in most seasons.

Methods

Fish used in the estimation of growth rate, mortality, and age-class structure were taken from the commercial fishery and from experimental gill nets containing 6 mesh sizes (3.8–10.2 cm, by 1.3-cm intervals). Spawning runs were sampled for 8 yr (1949–56) at traps in the Blackduck and Tamarack rivers and Mud Creek during walleye spawn-taking operations to determine growth rates and age-class distribution. Sampling from the commercial fishery was done on random boxes of fish taken from the lower lake after delivery to the sorting floor but before fish were graded or sorted. Since fishermen operate in all areas of the lower basin and the western half of the upper basin, the samples from the commercial fishery were considered to be representative of the population. Fish sampling was done annually from 1949 to 1973 throughout the fishing season.

Fishing effort was recorded as the number of 5-net lifts during the summer season. A unit of effort represents a lift of a 5-net unit (total length, 381 m) fished for one night, usually 12–16 h. All effort data have been adjusted to this unit since only 5 nets were permitted each fisherman in 1930–40; 8 nets thereafter. Age and growth determinations were made from fish scales by conventional methods, employing total body-length and scale-length relationships calculated for each species. Age-frequency distributions were extrapolated from samples aged to composite measurements from all fish handled. All data were originally taken and calculations made in English units and transformed to metric units for this report. All lengths are total lengths, from the tip of the snout to the farthest tip of the caudal fin. All net mesh sizes are extension measure.

Yield from the Commercial Fishery

Mean commercial yield of all species taken from the Red Lakes fishery was 489,733 kg in 1930–53 and 478,025 kg in 1954–75 (Table 1). Statistical summaries for the commercial fishery were divided into these two periods because a dam was constructed at the outlet of the lower lake in 1950, and high water levels and a severe decline in walleye abundance occurred at about this time. The annual yield of walleye and perch varied widely from year to year. Mean catch of number one walleye from 1930 to 1953 was 305,700 kg. Mean catch of "cull" walleye (fish weighing less than about 0.45 kg — usually 0.34 kg or less — or shorter than 36.8 cm) from 1943 to 1953 (not recorded in 1930–42) was 9,107 kg. From 1954 through 1975, the mean catch of number one walleye was 229,438 kg, and that of culls was 15,639 kg, or a total of 245,104 kg. Mean annual yield of yellow perch was 96,414 kg in 1930–53 and 109,532 kg in 1954–75 (Table 1). Total annual yield of all species was 4.193 kg/ha in the first period, of which walleye contributed 2.57 kg and perch 0.82; in the second period, the respective values were 4.192 kg for all species, 2.10 kg for walleye, and 0.94 kg for perch. Total catch of percoids declined about 10%, from 3.39 kg/ha in the first period to 3.04 in the second.

Fishing effort over the period recorded by the fishery cooperative ranged from 3,435 lifts in 1967 to 14,816 in 1943. The mean was 8,497 for 1930–53 and 8,513 for 1954–75. Annual variation expressed as percentage of mean effort for the 1930–40 period ranged from 57.6 to 248.4%. In the early years when walleye abundance was low, effort was usually relatively high and, conversely, in years of high abundance effort was relatively low. Because annual quotas of 295,100 to 454,000 kg of walleye were imposed in different years to limit maximum yield, fishing intensity tended to vary inversely with walleye abundance. From 1970 to 1975 fishing effort declined significantly in spite of low abundance because fishermen found more lucrative employment elsewhere (Table 2).

Fluctuation in Abundance of Walleye and Perch

Abundance of walleye (exclusive of culls) expressed as catch per unit of effort (CPE) has ranged from 3.8 kg in 1974 to 64.6 kg in 1967 (Table 2). Mean CPE for walleye was 34.6 kg in the 1930–53 period and 25.6 kg in 1954–75. Abundance in 1972–75 may not be directly comparable with that in other years because fishing was restricted to an area of the lake where late-season returns in some years were lower than the lake average. In the earlier years, when fishing was the only summer industry, competent fishermen remained active regardless of the abundance of walleye, but in more recent years the better fishermen have tended to stop fishing and seek more remunerative employment when abundance was low. Because prices for walleye were high in 1972–75, part of the catch may have been sold to outside traders, thereby reducing the catches recorded by the cooperative fishery in these years.

Perch abundance (CPE) varied from 0.4 kg in 1973 to 34.4 kg in 1968 (Table 2). The average was 11.8 kg in 1930–53 and 11.9 kg in 1954–75. The abrupt decline of both species in the 1970s, in addition to actual low abundance, may reflect the lack of fishermen to fish the lake areas where perch availability was commonly highest in earlier years.

Causes of Fluctuations in Abundance

The fluctuations in abundance of commercially available stocks of walleye and perch were caused primarily by changes in strength of year-classes, and by growth rates during the fishing season. In most years the commercial catches of both species were composed of fish of ages V, VI, and VII (Table 3). When weak year-classes appeared in these age-groups, abundance of available fish declined.

Cull walleye recorded in the catch statistics were predominantly age IV, which, with normal growth, became fully vulnerable to the commercial gear in the following 2 yr. To assess the validity of the assumption that abundance of commercially available fish was a function of year-class strength, and to further assess the value of estimation of cull abundance as a predictive tool, I correlated total annual yield and abundance (CPE) of cull walleye with catches and abundance of walleye 1 and 2 yr later. In four comparisons the correlation (*r*) was not significant at the 0.05 level.

The wide fluctuation of growth rate of walleye in individual seasons, shown below, appeared to have more influence on recruitment in the particular season than did the actual abundance of cull walleye in the previous seasons. Correlation between growth rate in any season, expressed as percentage deviation from mean growth to the period, and yield in the same year was significant ($r = 0.594$, $P < 0.05$).

The possibility of a reciprocal relation between the relative abundance of perch and walleye was recognized, but correlation between abundance (CPE) of commercially available fish of the two species ($r = 0.368$, $P < 0.01$) was positive. Correlation of fishing effort (Table 2) in the season before the season of catch with walleye abundance was negative ($r = -0.290$), but not significant at the 0.05 level.

When the influence of fishing effort on perch yield was tested by correlating catch with fishing effort in the previous year, the correlation was not significant. Growth rate of perch in the

TABLE 2. Total summer lifts (5-net units) and average catch (kilograms) per lift of walleye, perch, and total of all species, 1930–75.

Year	Average fishermen per night	Total summer lifts	All species	Walleye	Walleye cull	Total walleye	Perch
1930	—	6,586	38.7	27.7	—	27.7	5.1
1931	—	5,794	51.3	40.9	—	40.9	6.1
1932	—	3,860	71.7	50.3	—	50.3	15.2
1933	—	5,417	58.9	40.9	—	40.9	14.9
1934	—	6,672	45.4	30.0	—	30.0	10.5
1935	—	7,087	37.4	18.5	—	18.5	9.5
1936	—	7,842	40.0	15.3	—	15.3	6.6
1937	—	5,172	74.1	43.7	—	43.7	19.7
1938	86	4,910	82.9	53.1	—	53.1	18.8
1939	110	5,657	71.3	43.4	—	43.4	15.3
1940	120	6,614	70.2	46.3	—	46.3	10.9
1941	117	8,086	58.6	43.4	—	43.4	5.1
1942	172	12,934	44.8	32.8	—	32.8	5.8
1943	91	14,816	37.6	23.8	1.2	25.0	5.9
1944	92	8,454	68.3	45.1	0.9	46.0	16.8
1945	108	10,596	55.5	33.1	0.7	33.8	12.8
1946	130	11,092	51.9	33.1	0.8	33.9	12.2
1947	157	12,393	50.1	31.7	1.3	33.0	11.5
1948	190	10,083	60.4	41.3	0.3	41.6	11.3
1949	182	9,905	48.5	29.1	1.1	30.2	8.5
1950	150	12,768	23.2	13.8	0.6	14.4	2.5
1951	105	12,449	27.6	20.3	0.4	20.7	4.1
1952	148	7,856	64.6	37.8	0.7	38.5	23.0
1953	187	6,883	69.6	35.5	1.3	36.8	29.9
1954	160	7,918	68.4	36.4	1.3	37.7	28.2
1955	150	9,373	50.0	28.5	1.0	29.5	16.0
1956	138	10,835	37.5	23.6	0.4	24.0	7.6
1957	156	8,723	51.3	34.2	0.6	34.8	11.2
1958	171	14,493	30.9	19.3	1.3	20.6	5.8
1959	162	14,802	39.0	14.8	4.1	18.9	6.9
1960	169	12,160	41.3	20.4	3.2	23.6	8.4
1961	199	5,416	78.8	55.7	0.5	56.2	13.7
1962	176	6,768	61.0	50.4	0.2	50.6	13.1
1963	152	9,752	43.2	17.4	0.9	18.3	13.2
1964	111	9,090	48.4	23.8	4.1	27.9	10.1
1965	79	11,478	35.2	13.5	5.5	19.0	12.4
1966	97	9,090	58.7	38.7	2.0	40.7	13.8
1967	113	3,435	94.6	64.6	1.7	66.3	22.1
1968	91	5,083	80.9	39.9	2.0	41.9	34.4
1969	86	10,013	44.1	19.5	1.0	20.5	17.2
1970	100	10,256	40.0	23.7	0.3	24.0	7.9
1971	109	10,984	30.3	15.0	1.5	16.5	4.2
1972	46	5,382	22.8	4.6	1.2	5.8	0.7
1973	29	4,813	22.9	5.0	0.1	5.1	0.4
1974	31	3,613	32.0	3.8	3.5	7.3	7.1
1975	36	3,800	33.0	11.3	0.2	11.5	7.8
1930–53 Means	134.1[a]	8,499	59.2	34.6	0.8[b]	38.2	11.8
1954–75 Means	106.7	8,513	43.5	25.6	1.5	25.0	11.9

[a] Includes data from 1938 to 1953 only.

[b] Includes data from 1943 to 1953 only.

season of catch was significantly correlated at the 0.05 level ($r = 0.500$) with perch abundance (CPE). When abundance of all species other than walleye was compared with abundance of walleye in the same fishing season, the correlation was positive and highly significant ($r = 0.606$, $P < 0.01$), rather than negative. Since perch are a major contributor to the total catch and their

TABLE 3. Age distribution of perch and walleye in the commercial catch, expressed as percentage of total fish of each of these species caught, 1949–64.

	Age-class							
	IV		V		VI		VII	
Year	Walleye	Perch	Walleye	Perch	Walleye	Perch	Walleye	Perch
1949	8.7	6.3	35.2	19.0	32.0	32.4	1.8	12.1
1950	29.1	33.0	13.9	27.2	22.1	20.5	20.2	14.1
1951	17.5	20.7	64.0	53.4	6.8	15.9	4.4	8.1
1952	3.9	1.7	46.0	33.5	41.7	56.5	2.6	5.7
1953	3.5	0.0	12.1	1.0	52.6	51.9	28.1	42.2
1954	2.3	0.1	14.7	2.1	21.4	7.7	43.3	58.9
1955	3.5	3.0	11.4	3.1	24.6	10.9	20.1	11.1
1956	6.3	1.3	15.9	10.3	25.0	7.5	26.2	13.1
1957	9.1	5.5	27.4	2.8	22.5	19.5	17.6	9.1
1958		21.1		7.9		11.5		12.8
1959		20.4		38.0		9.3		6.7
1960		21.0		36.7		30.7		5.6
1961		6.0		35.0		33.3		19.6
1962		1.2		8.7		49.0		24.3
1963		11.7		2.6		7.6		40.8
1964		37.1		13.5		6.3		5.4

abundance during a given season is closely correlated with that of walleye, the apparent absence of inhibition on walleye abundance by other species was expected.

Catch Composition

As noted above, the commercial catch of walleye and perch in most years was made up principally of ages V, VI, and VII. In some years age IV fish of both species made up a substantial portion of the catch. This shift usually resulted when year-classes representing older age-groups were weak or the year-class representing age IV was exceptionally strong.

Lengths of 113,242 walleyes caught in commercial gear in 1949–57 ranged from 20.3 to 60.7 cm; almost 55% of the fish were 35.5 to 39.4 cm long (Table 4). Maximum vulnerability to the gear was at a length of about 38.4 cm. Mean weight of fish at this length was 499 g. A comparison of length frequencies of fish in spawning runs with frequencies in the commercial catch (Smith and Pycha 1961) indicated that the vulnerability of fish to the commercial gear decreased after the fish exceeded a certain size; large fish are relatively more plentiful in the spawning run than in the segment of the commercial catch consisting of fish presumed to be mature.

Perch in the commercial catch were 17.8 to 31.2 cm long. Maximum vulnerability, estimated from 103,448 fish collected over 16 yr (1949–64) was at lengths of 25.4 to 26.2 cm. The length frequency distribution varied from year to year, since the commercial gill nets were not highly selective, and the catch was strongly influenced by relative strength of year-classes (Heyerdahl and Smith 1971). Average weight at 25.4 cm was 255 g.

Year-Class Strength of Perch and Walleye

Relative strengths of year classes in both perch and walleye varied over a large range. Strengths of year classes in walleye (Table 5) were estimated for the period 1942–56 from the number of fish of age-groups IV to IX taken per 100-nets lifted and from total return to the fishery. Estimates of strength of year-classes of perch were made from total returns of each year-class to the fishery in 1942–60 (Table 5).

When a series of correlations of year-class strength in both species with potential factors influencing it were calculated, the highest correlation was found between strengths of walleye and perch year-classes that originated in the same year of hatch. Comparisons of year-class strength with climatic factors in a number of combinations during incubation and early life of the fish (fry and fingerlings) failed to yield significant correlations. Since the two species varied together, I postulate that early spawning followed by a cool period retarded incubation and decreased successful hatch. General observations on climatic conditions supported this suggestion. I further suggest that temperature also acted through its influence on food availability to fry and on successful early feeding of fry and fingerlings.

Laboratory experiments (Koenst and Smith

TABLE 4. Percentage of total catch of 113,242 walleyes from commercial gear in different length intervals,[a] 1949–57.

Interval length (cm)	Percentage	Interval length (cm)	Percentage
20.3–23.2	0.02	39.5–40.4	9.46
23.3–24.2	0.03	40.5–41.5	7.18
24.3–25.2	0.08	41.6–42.5	4.44
25.3–26.2	0.08	42.6–43.5	3.02
26.3–27.2	0.20	43.6–44.5	1.92
27.3–28.2	0.26	44.6–45.5	1.19
28.3–29.3	0.52	45.6–46.5	0.89
29.4–30.3	0.73	46.6–47.6	0.62
30.4–31.3	1.08	47.7–48.6	0.48
31.4–32.3	1.29	48.7–49.6	0.21
32.3–33.3	1.77	49.7–50.6	0.25
33.4–34.3	2.98	50.7–51.6	0.18
34.4–35.4	6.18	51.7–52.6	0.11
35.5–36.4	11.20	52.7–53.6	0.07
36.5–37.4	14.63	53.7–54.7	0.03
37.5–38.4	15.61	54.8–55.7	0.02
38.5–39.4	13.19	55.8–60.7	0.02

[a] Measurements were made in inches; metric intervals are closest approximation to original intervals.

TABLE 5. Year-class strength expressed as percentage of mean strength for the period 1942–56 (walleye) or 1942–60 (perch) and back-calculated total length at age I of the respective year-classes.

	Walleye		Yellow Perch	
Year	Strength of year-class	Length at annulus I (mm)	Strength of year-class	Length at annulus I (mm)
1942	10	118	37	65
1943	145	136	49	66
1944	83	142	35	64
1945	23	137	42	63
1946	174	141	320	68
1947	232	143	406	61
1948	81	150	51	63
1949	79	146	47	63
1950	62	136	20	54
1951	67	140	36	63
1952	103	142	15	56
1953	56	134	23	75
1954	174	135	98	68
1955	81	142	119	75
1956	43	124	154	68
1957	—	—	27	—
1958	—	—	18	—
1959	—	—	36	—
1960	—	—	366	—

1976) on temperature responses of walleye eggs, fry, and fingerlings showed that temperatures rose above the optimum for egg incubation (9–15°C) before fry initiated feeding behavior. Without such an increase, fry did not start feeding, even in the presence of abundant plankton, and consequently died when the yolk was absorbed. Similar information is not available for perch, but Kenneth Hokanson (personal communication) stated that unpublished laboratory data suggest similar requirements for perch fry and fingerlings.

The abundance of adult stock in both species, as determined by CPE during the season, was not significantly correlated with respective year-class strength. Rate of growth during the first year of life in perch and walleye (Table 5) was considered as a possible factor determining success of a year-class. In walleye there was an apparent positive influence ($r = 0.411$), but it was not significant. In perch the correlation was lower and again not significant. When the perch and walleyes of year-classes 1945–54 were compared, the correlation was high ($r = 0.858$, $P < 0.01$). Years of best hatch were those in which spawning occurred about midway between the extremes of the spawning season and the later increase in water temperature was uniform and gradual.

Growth of Walleye

Walleye growth in the Red Lakes was determined from 17 year-classes (1940–56) collected during 8 calendar years (1949–56). Nine age-groups were used; older fish were omitted because the sample was small. A total of 5152 fish were used, of which 3539 came from experimental gill nets and the rest from fish caught in spawning runs by hatchery craft. Comparison of fish lengths back-calculated from commercial nets with those back-calculated from fish caught in experimental nets and spawning runs indicated no significant differences. All calculations reported here were made from samples taken in the lower basin; however, Smith and Pycha (1961) determined that fish taken from both the upper and lower lakes had the same growth patterns. Grand average calculated total lengths of male and female walleye were the same through the fourth year, and then diverged as females began growing more rapidly (Table 6). At age IX, females were 46.5 cm long and weighed 899 g, and males were 42.0 cm long and weighed 654 g. Females are fully vulnerable to the gear in the sixth season of growth (age V) and males after the formation of the seventh growing season (age VI) or later. Because individual growth varied widely and gill nets select from a relatively broad length range, recruitment of both sexes to the fishery occurs over a 2–3-yr period. Recruitment of females to the fishery about a year earlier than recruitment of males, and earlier maturity of

TABLE 6. Mean total length and weight of 3083 male and 2069 female walleye from the 1940–56 year-classes at the time of annulus formation, at ages I–IX.

	Males		Females	
Annulus	Length (cm)	Weight (g)	Length (cm)	Weight (g)
I	14.0	22	14.1	227
II	21.1	82	21.1	82
III	26.7	163	26.7	163
IV	31.1	263	31.2	268
V	34.4	359	34.9	372
VI	36.8	431	38.2	490
VII	38.6	508	41.0	608
VIII	40.4	586	43.5	736
IX	42.0	654	46.5	899

males, may account for the divergence in sex ratio in spawning runs, where males exceeded females in an approximate ratio of 3 to 1.

The percentage annual increment in total length decreased rather steadily from 50.5% in females and 51.3% in males during the second growing season to 6.9% in females and 3.8% in males during the ninth growing season.

Growth rate of walleyes in different calendar years varied from −42.2% of the mean growth rate for 1941–56 (in 1950) to +30.7% (in 1947; see Table 7). Time of annulus formation was progressively delayed as fish advanced in age; (Table 8; Smith and Pycha 1961). Annulus formation in a year of good growth (1951) started during the week of June 13–19; was completed in group III in the week of June 27–July 3; in groups IV, V, and VI in the week of July 4–10; and in age-group VII in the week of July 25–31. In 1953, a year of poor growth, annulus formation was not completed until the week of August 1–7 in group V and after August 15–21 in older fish.

Rate of growth within a season varied with total growth for the year (Table 8). In the good-growth year of 1955, there was no trend among age-groups in growth completed by a particular date. By the second week in August, 49–66% of the seasonal growth was completed, and by the third week 63–78% was completed in age-groups III–VII (Table 8). In 1956, a year of poor to moderate growth, 69–100% of growth in all groups was completed by the third week in August. In a few instances total growth increment in older fish at the close of the growing season was greater than the mean increment measured at the time of formation of the next annulus. This apparent anomaly is the result of differences in sampling or in mortality during the winter and at spring spawning. In general, females completed annual growth sooner than males, especially among older fish.

Length–weight relation of 1604 walleyes 16.3 to 55.9 cm long, taken throughout the season was expressed by the formula (Smith and Pycha 1961): $W = 0.002786\ L^{3.04957}$.

Growth of Perch

Perch growth in lower Red Lake was derived from 4260 fish representing 17 year-classes taken in 8 calendar years (1949–56). All fish were taken in experimental gill nets. Total length of males and females was the same at the time of age II (13.2 cm), but thereafter females grew faster. At age X, males were 24.9 cm long and females 27.4 cm long (Table 9). Males at age X weighed 250 g and females 218 g. Most fish became fully vulnerable to commercial gear during their sixth growing season (age V) at 25.9 cm. As in walleyes, the females were vulnerable to the gear about 1 yr earlier than males. Growth variations between year-classes were great (Heyerdahl and Smith 1971). For example, at age V, length of males varied from 20.8 to 23.1 cm and that of females from 22.6 to 25.1 cm in different year-classes. Therefore growth history of each year-class is more significant to determine age of recruitment than seasonal growth rate during the year of catch.

Mean growth of perch in different calendar years (1950 excepted) varied less than in walleye, ranging from +13.4 to −8.6% of mean annual growth for the entire period of study (Table 7). Annual growth rate, therefore, had little influence on annual recruitment to the commercially available stock in any year.

Length–weight relation derived from measurements in inches and ounces of 14,169 fish are described by two formulas from Heyerdahl and Smith (1971):

$$\log W = -2.4736 + 3.07837 \log L$$

for fish 9.4–22.6 cm long and

$$\log W = -1.71835 + 2.64898 \log L$$

for fish 22.9–31.8 cm long

Discussion and Implications for Management

Evaluation of data covering a 27-yr period (1949–75) suggested some important implications for management of the Red Lakes fishery. The most important was based on the relation of seasonal growth and availability of walleyes to the commercial gear, and hence to total annual production. As noted, there was a high correlation between growth and availability within a season. In contrast, perch, which vary less in annual growth rate, showed only a weak relation between growth rate and commercial availability. Strength of individual year-classes was not a good pre-

TABLE 7. Percentage deviation from mean annual growth of walleyes and perch 1941–56[a]

	Walleye			Perch		
Year	Male	Female	Mean	Male	Female	Mean
1941	+ 6.2	+ 7.0	+ 6.6	+ 2.3	—	+ 2.3
1942	−24.5	−25.0	−24.8	+ 6.2	+ 9.7	+ 7.9
1943	+21.9	+22.7	+22.8	+ 1.0	+ 4.5	+ 2.7
1944	+18.6	+20.2	+19.4	+ 7.3	+ 0.9	+ 4.1
1945	−17.2	−22.1	−19.7	+ 4.6	+ 3.3	+ 3.9
1946	+ 5.6	+11.8	+ 8.7	+ 3.7	+ 4.3	+ 4.0
1947	+29.2	+32.2	+30.7	+ 1.9	+ 4.0	+ 3.0
1948	+25.9	+25.1	+25.5	− 0.1	+ 2.6	+ 1.3
1949	+ 4.2	+ 0.5	+ 2.4	− 8.0	− 9.3	− 8.6
1950	−42.8	−41.5	−42.2	−52.1	−53.4	−52.7
1951	+ 3.8	+ 2.9	+ 3.4	+13.7	+13.2	+13.4
1952	− 3.7	0.0	− 1.8	+ 2.1	+ 4.6	+ 3.4
1953	−30.1	−33.8	−31.9	+ 9.3	+ 7.9	+ 8.6
1954	− 3.0	− 6.0	− 4.5	+ 3.4	+ 2.1	+ 2.7
1955	+ 8.4	+ 6.5	+ 7.5	+ 4.4	+ 2.3	+ 3.4
1956	− 2.5	− 0.3	− 1.4	+ 0.3	+ 3.2	+ 1.8

[a] Based on calculated length of all fish used for growth determination (Table 6).

TABLE 8. Cumulative growth in length of walleye of age-groups III–VII expressed as percentage of entire season's growth for successive weeks from July 11 to August 21 in 1955 and 1956.

Year and week	Sex	Age-group				
		III	IV	V	VI	VII
1955						
July 11–17	Male	28	24	10	—	8
	Female	12	18	37	25	14
July 18–24	Male	36	33	39	20	—
	Female	30	18	30	29	22
July 25–31	Male	34	37	56	25	0
	Female	41	59	28	28	80
Aug. 8–14	Male	61	49	61	58	51
	Female	64	60	58	66	64
Aug. 15–21	Male	66	63	71	63	31
	Female	63	67	69	75	78
1956						
July 11–17	Male	9	42	34	—	43
	Female	—	—	42	—	46
July 18–24	Male	—	25	52	—	54
	Female	41	46	54	75	83
July 25–31	Male	61	51	60	66	38
	Female	46	59	57	38	63
Aug. 8–14	Male	57	43	68	52	46
	Female	55	57	70	53	54
Aug. 15–21	Male	87	69	78	90	91
	Female	70	80	123	107	74

dictor for harvestable stock in either species because recruitment was spread over several age-groups, and total growth of individuals in a year-class before availability to the commercial gear varied over a considerable range. Although general trends in availability could be predicted, useful predictions could be made only after a fishing season is underway.

The contribution of individual year-classes to the fishery was not closely related to the size of parent stock during the years of observation; consequently the rate of fishing did not control later population abundance. Because annual recruitment of walleyes and perch to the fishable stock depended to a large extent on growth during the fishing season, fishing intensity during

TABLE 9. Mean total length and weight at successive annuli of 2133 male and 2127 female perch from the 1940–56 year-classes.

	Males		Females	
Annulus	Length (cm)	Weight (g)	Length (cm)	Weight (g)
I	7.4	5.7	7.4	5.7
II	13.2	34.0	13.2	34.0
III	17.3	73.7	17.8	85.1
IV	20.1	121.9	21.8	153.1
V	22.1	161.6	24.1	212.6
VI	23.4	198.5	25.4	243.8
VII	24.1	212.6	26.2	266.5
VIII	24.4	229.6	26.7	289.2
IX	24.6	238.1	26.7	300.5
X	24.9	249.5	27.4	317.5
XI	25.4	266.5	—	—

TABLE 10. Annual increment in total length and weight of walleye and perch expressed as percentage growth between succeeding annuli, 1940–56 year-classes.

	Walleye		Perch	
Annulus	Length (cm)	Weight (g)	Length (cm)	Weight (g)
I II	51.3	256.0	81.0	515.9
III	26.2	103.4	32.4	139.8
IV	16.8	60.5	19.4	71.4
V	10.4	35.5	10.3	36.6
VI	6.4	20.7	5.5	18.2
VII	5.6	17.9	3.1	8.4
VIII	4.7	15.2	2.5	7.9
IX	3.8	11.9	1.5	2.3

one season did not cause major changes in yield of subsequent seasons. Strength of year-class in both perch and walleye appeared to be determined principally by climatic conditions rather than by other factors. The exact mechanism of this relation was not defined, but temperature regimes during and after spawning seemed to be a major factor.

Increment in weight (Table 10) and a rough approximation of natural mortality rates (Smith and Pycha 1961; Heyerdahl and Smith 1971) of 20–23% in both perch and walleyes in Red Lakes indicated that perch should be taken during their fifth season of growth (age IV) and walleye during the sixth season (age V). Total mortality was 65–70% for walleye (Smith and Pycha 1961) and 57% for perch (Heyerdahl and Smith 1971). In certain years when large year-classes of walleye were in the fishery, a heavier fishing effort could probably have been supported without detriment to the stock; but, on the average, the exploitation rates appeared to be large enough to prevent potential loss in production. Because average size of perch at capture was above the critical size for theoretical maximum yield, they could apparently sustain heavier cropping and consequently increased annual production. As long as the gillnet fishery is carried on with the mesh size used in 1930–75 and walleye quotas govern the total annual effort, increased effort on perch is not possible. Use of entrapment gear which would take more and smaller perch without destroying undersized walleye could raise the annual production of perch.

In view of the importance of in-season growth on availability and increment of the harvestable stock of walleye, a delay in the start of fishing until after July 1 might result in greater annual production.

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Trends in Percid Yields from Lake of the Woods, 1888–1973[1]

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Commercial yields of walleye (*Stizostedion vitreum vitreum*) increased from 1888 to the mid-1930s and then gradually declined to 1973. Commercial yields of sauger (*S. canadense*) and yellow perch (*Perca flavescens*), first recorded in 1926, were more stable than walleye yields. The increase in walleye yields was associated with declines in the yield of lake sturgeon (*Acipenser fulvescens*) and lake whitefish (*Coregonus clupeaformis*). Walleye yields declined from 1.7 kg·ha^{-1} annually in the 1930s to 0.8 kg·ha^{-1} during 1964–73. Exploitation by commercial and sport fisheries appeared to be the main cause of the decline. Creel surveys from 1967 to 1971 indicated that the sportfishing yield exceeded the commercial yield, and the combined harvest was near the high levels in the 1930s. Wider fluctuations in yield observed since the 1950s suggested that recruitment had become more variable. Short-term increases in growth rate were observed in one area after intensive walleye harvests, but in other parts of the lake no change in growth rates was observed. Sauger appeared to be increasing in abundance in the northern areas of the lake, probably in response to increasing turbidity.

Key words. Percidae, yield trends, *Stizostedion*, *Perca*, harvest

SCHUPP, D. H., AND V. MACINS. 1977. Trends in percid yields from Lake of the Woods, 1888–1973. J. Fish. Res. Board Can. 34: 1784–1791.

Les rendements commerciaux en dorés jaunes (*Stizostedion vitreum vitreum*) augmentèrent de 1888 au milieu des années 1930, pour ensuite diminuer graduellement jusqu'en 1973. Les rendements commerciaux en dorés noirs (*S. canadense*) et en perchaudes (*Perca flavescens*) enregistrés pour la première fois en 1926, ont été plus stables que ceux du doré jaune. On associe l'augmentation des rendements en dorés jaunes au déclin des rendements en esturgeons (*Acipenser fulvescens*) et en grands corégones (*Coregonus clupeaformis*). Les rendements en dorés jaunes diminuèrent de 1.7 kg·ha^{-1} annuellement durant les années 1930 à 0.8 kg·ha^{-1} durant la période de 1964–73. La principale cause du déclin semble être l'exploitation par les pêches commerciale et sportive. Des recensements au panier effectués entre 1967 et 1971 indiquent que le rendement de la pêche sportive dépassait celui de la pêche commerciale, et que la récolte combinée se rapprochait des hauts niveaux des années 1930. Les plus grandes fluctuations observées dans le rendement depuis 1950 suggèrent que le recrutement est devenu plus variable. On a observé des augmentations à court terme du rythme de croissance dans une région à la suite de récoltes intensives de dorés jaunes; mais dans d'autres parties du lac, aucun changement n'a été observé dans le rythme de croissance. Le doré noir a semblé augmenter d'abondance dans les régions septentrionales du lac, probablement en réponse à une augmentation de la turbidité.

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TRENDS in percid yields from 1888 to 1973 from Lake of the Woods are described. Commercial catch data are the only information available from which to draw conclusions about long-term trends and changes in the fish communities of Lake of the Woods. Carlander (1942) and Heyerdahl and Smith (1972) described changes in the Minnesota fishery. Data from these sources and official records from Ontario and Minnesota maintained since the inception of the fishery, are used in this paper to review trends throughout the lake. Available data provide no long-term record of CPE which might reflect changes in abundance. Records on total fishing effort are available from Minnesota from 1949 to 1973 and only partial records are available from Ontario since 1964.

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Creel surveys from 1967 to 1971 on both sides of the border provided some measure of sportfishing harvest.

Percids are an important component of the fish fauna in the lake and economically are the most valued family. Seven percids are found: walleye (*Stizostedion vitreum vitreum*), sauger (*S. canadense*), yellow perch (*Perca flavescens*), log perch (*Percina caprodes*), Johnny darter (*Etheostoma nigrum*), Iowa darter (*Etheostoma exile*), and river darter (*Percina shumardi*).

Lake Description and Physiography

Lake of the Woods lies on the border between northwestern Ontario and southeastern Manitoba, Canada, and northwestern Minnesota, USA. Two-thirds of the water, including Shoal Lake, is in Canada (Fig. 1). Although irregular in shape, the lake at its widest spans 105 km in a north–south direction and 90 km east and west.

The lake is on the Precambrian shield. The southwestern portion, known as the Big Traverse, was part of glacial Lake Agassiz (Schwartz and Thiel 1963). Occasional outcroppings of rock are still evident about southwestern portions, but most of the lake bottom and the surrounding land is covered with lake sediments. Most of Ontario's waters have steep, rocky shores indented by numerous bays and inlets and contain nearly all of the many islands.

The lake is relatively shallow. The average depth has been estimated at 7.9 m (Table 1). The maximum recorded depth (65.8 m) is in Whitefish Bay. Rainy River is the principal tributary, contributing over 75% of the inflow. Water from the lake flows north to Hudson Bay through three outlets near Kenora. Dams at the two principal outlets regulate water levels and generate electricity. Under these controlled conditions, water levels fluctuate between 0.9 and 1.2 m annually.

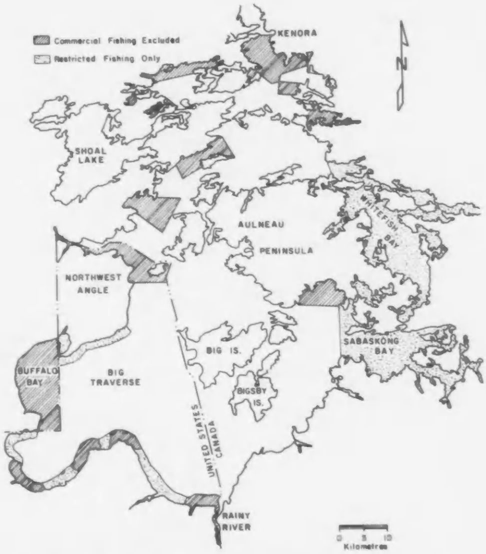

FIG. 1. Distribution of commercial fishing zones in Lake of the Woods.

TABLE 1. Physical and chemical characteristics of Lake of the Woods.

Latitude	49° N
Watershed area	70,030 km^2
Water area	3,850 km^2
Mean depth	7.9 m
Maximum depth	65.8 m
Shoreline development factor	1.7
Transparency (Secchi disc)	0.6 m
Growing season	170 days
Annual precipitation	610 mm
Morpoedaphic index	10.5
Total dissolved solids	45–138 $mg \cdot \ell^{-1}$
Total alkalinity	32–92 $mg \cdot \ell^{-1}$
Inorganic turbidity (silica)	0.2–8.0 $mg \cdot \ell^{-1}$

The lake is mesotrophic. Total dissolved solids range from 45 $mg \cdot \ell^{-1}$ in Whitefish Bay to 138 $mg \cdot \ell^{-1}$ in the Big Traverse. The morphoedaphic index (Ryder 1965), based on an average TDS of 83 $mg \cdot \ell^{-1}$ and a mean depth of 7.9 m is 10.5. Adams and Olver (1977) calculated the MEI for Ontario waters to be 9.6; the value for Minnesota waters, based on information from Carlander (1942), is 18.6. Minnesota waters are shallower and more turbid.

Water transparency is low in most areas. During August, a Secchi disc is visible at 0.6 m in the southern part and at 5.5 m in Whitefish Bay. The low transparencies in August are caused by dense blooms of blue-green algae (mainly *Aphanizomenon flosaquae*). Most of the lake does not stratify thermally.

History of the Fisheries

Demands on resources of the lake were limited before the coming of white men. Indians living near the lake did little to affect the lake or its tributaries. The establishment of the fishing industry and of paper mills and the construction of dams were followed by changes that nearly eliminated once-important species of fish and adversely affected others.

The commercial fisheries developed along roughly parallel lines on the two sides of the border. Development was modified by the different morphoedaphic characteristics of the U.S. and Canadian waters and the two political jurisdictions. The international boundary provides a nearly exact separation of the morphoedaphic characteristics, which influence the kind and amount of gear fished, catch composition, mean yield, and management policy.

Commercial fishing began by 1888 on the U.S. side, with no restrictions (Carlander 1942). On the

Canadian side, the lake was opened to commercial fishing in 1892. Licenses limited the holder to one pound net and 914 m of gill net. Restrictions on the U.S. side were introduced in 1895, permitting each licensee to fish 50 pound nets. At one time, more than 300 pound nets were being fished.

Lake sturgeon (*Acipenser fulvescens*) and lake whitefish (*Coregonus clupeaformis*) were the most important species in the early years but, as catches fluctuated, fishermen on the Ontario side received an increased gear allowance of 5 pound nets per licensee. Gear allowances on the Minnesota side were reduced to 25 pound nets in 1911 and to 6 per licensee in 1925.

Gill nets were authorized for Minnesota waters in 1911, but the first record of licensed gill nets was in 1917, for 22,900 m. These versatile nets were used with increasing frequency and by 1950 about 70% of the Minnesota harvest was taken by gill nets. Most of the Ontario commercial harvest since 1900 was also taken by gill nets. The long-term trends in commercial production from Minnesota and Ontario waters has been upward since the earliest days of the fishery (Fig. 2). Interruptions in the trend occurred in response to changes in abundance of some species, changing regulations, and economic conditions. The only near stable period of production was from the mid-1920s through the 1930s in Ontario.

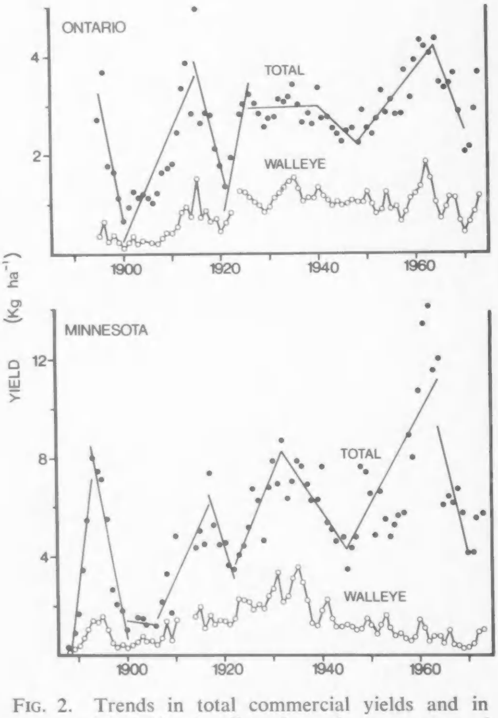

FIG. 2. Trends in total commercial yields and in commercial yields of walleye from the two waters of Lake of the Woods, 1888–1973. Solid lines are linear regressions of total yield on time for the years indicated in Table 2.

Commercial production from Ontario reached the theoretical annual yield (3.8 kg·ha^{-1}) only from 1958 through 1964, as a result of substantial increases in the harvest of cisco (*Coregonus artedi*), burbot (*Lota lota*), and white sucker (*Catostomus commersoni*), and a more intensive harvest from Shoal Lake. The theoretical yield from Minnesota (5.1 kg·ha^{-1}) was exceeded in most years from 1925 to 1973. From 1958 through 1964, the Minnesota commercial fishery harvested an average of 10.1 kg·ha^{-1}, most of it being due to an increase in the harvest of cisco.

Improved highways and development of faster boats increased the mobility of anglers and led to greater sportfishing pressure. Intermittent estimates of the annual sportfishing harvest from 1967 to 1971, when added to the commercial harvest, indicate that the theoretical yield was exceeded on both sides of the border in recent years.

Inevitably, conflicts between commercial and sportfishing arose, especially over the harvest of walleye. Investigations by Carlander (1942), Burrows (1951), Scidmore (1963), Heyerdahl and Smith (1972), and Schupp (1974) were explicitly or implicitly involved with competition between commercial and sportfishing in Minnesota. Ontario has assigned a biologist to monitor fish stocks in the Ontario waters since 1964.

Further restrictions were imposed on the fish harvest through the years. At first, these were mainly efforts to maintain viable stocks for commercial fishing. More recently, regulations governing the location of nets and time of fishing have been imposed on the commercial fishery to favor the sport fishery.

Pulp mills were constructed at International Falls in 1907 and Fort Francis in 1914. Until recent years, all wood fiber wastes from these mills were disposed of in the Rainy River. Deposits of these wastes are present throughout the 130 km length of the river in areas of slow current and extend up to 5 km into the lake in the main current. Four-mile Bay, a shallow bay (3 m) of about 12,000 ha, is the delta of the Rainy River. As much as 25% of the bay bottom is covered with wood-fiber wastes.

Walleye

Trends in commercial production of walleye did not parallel the rising trends in total production from Minnesota and Ontario waters. Walleye yields generally increased from 1900 to 1935 and declined to 1973 (Fig. 2). When combined, Canadian and U.S. commercial walleye yield averaged 1.7 kg·ha^{-1} annually in the 1930s, reaching a high of 2.2 kg·ha^{-1} in 1935. From 1964 through 1973, the combined yield averaged 0.8 kg·ha^{-1} annually. The rate of decline was greater in Min-

TABLE 2. Trends in commercial fish yields from Lake of the Woods and correlations between yields of various species and total yields.

Years in trend	Direction of trend	Trend direction correlation	Walleye	Lake sturgeon	Lake whitefish	Other[c] species
		ONTARIO				
1895–1900	Declining	−0.878[a]	0.936[a]	0.980[a]	0.924[a]	0.423
1900–1915	Rising	0.874[a]	0.997[a]	0.506[b]	0.868[a]	0.464
1915–1921	Declining	−0.820[b]	0.924[a]	0.933[a]	0.718	0.881
1921–1926	Rising	0.981[a]	0.943[b]	0.439	0.917[b]	0.930[b]
1926–1940	Stable	0.068	0.814[a]	−0.489	0.267	0.846[a]
1940–1948	Declining	−0.791[b]	0.895[a]	—	0.583	0.665
1948–1964	Rising	0.878[a]	0.659[a]	0.471	−0.665	0.957[a]
1964–1970	Declining	−0.819[b]	0.807[b]	0.161	0.621	0.979[a]
		MINNESOTA				
1888–1893	Rising	0.969[a]	0.996[a]	0.998[a]	0.998[a]	—
1893–1900	Declining	−0.965[a]	0.976[a]	0.983[a]	0.901[a]	—
1900–1906	Stable	−0.238	0.485	0.413	0.827[b]	—
1906–1917	Rising	0.900[a]	0.811[a]	−0.541	−0.445	0.630
1917–1922	Declining	−0.912[b]	0.497	—	0.867[a]	0.983[a]
1922–1932	Rising	0.892[a]	0.486	—	−0.385	0.961[a]
1932–1945	Declining	−0.846[a]	0.654[b]	—	0.721[a]	0.770[a]
1945–1964	Rising	0.748[a]	−0.393	—	−0.392	0.977[a]
1964–1970	Declining	−0.749	0.438	—	−0.524	0.994[a]

[a] $P < 0.01$.

[b] $P < 0.05$.

[c] Yellow perch, sauger, lake trout, cisco, northern pike, bullhead, burbot, black crappie.

nesota than in Ontario. Linear regressions of yield on time indicated an average annual decline of 0.01 kg·ha^{-1} (1,889 kg) for Ontario ($r = -0.311$, $P < 0.05$) and 0.04 kg·ha^{-1} (5,632 kg) for Minnesota ($r = -0.745$, $P < 0.01$) from 1935 through 1973.

The gradual rise in walleye yield from 1900 to 1935 was probably unrelated to changes in abundance. Periods of rising and declining total yields ranging from 6 to 20 years can be identified within the major rising trend for both Ontario and Minnesota (Fig. 2). Correlations of yields of individual species with total yields (Table 2) within the minor trends suggest that walleye yields were usually more closely related to rises than to declines in the early years. In contrast, sturgeon and whitefish yields were usually more closely related to declines. This suggests that walleye were not being harvested to their full potential until the more valued sturgeon and whitefish had been depleted and there was a shift from impoundment gear to entangling gear.

There is also evidence to suggest that the long-term decline in walleye yields beginning in 1935 was unrelated to changes in abundance. The decline in commercial walleye yields from Minnesota was partly a result of a statutory reduction in the amount of gill nets licensed in 1947 and halting the issuance of new licenses in 1948 (Fig. 3). Furthermore, growth rates for walleye from Minnesota waters in 1968–70 (Heyerdahl and Smith 1972) were similar to those reported by Carlander (1942) in 1939–41.

The harvest of walleye by a growing sport fishery may have supplanted the commercial harvest in part, with no net change in total yield. Two estimates of the annual angling harvest in Ontario (1967 and 1971) ranged from 1.0 to 1.6 kg·ha^{-1}. Estimates in Minnesota in 1968–70 ranged from 0.9 to 1.6 kg·ha^{-1} (Schupp 1974). The mean of these intermittent estimates was 1.2 kg·ha^{-1}. The addition of the mean annual commercial harvest for 1964–73 indicates an average annual harvest of 2.0 kg·ha^{-1} in recent years. This approximates the 1935 commercial yield of 2.2 kg·ha^{-1}.

There are, however, indications that the decline in commercial walleye yield was accompanied by changes in the population. The correlations of walleye yields with total yields were higher for declines than for rises from the 1930s to 1973 (Table 2). Walleye yields in Ontario were still significantly correlated with total yields, but in Minnesota walleye yields declined from 1945 to 1964 though total yield increased.

The trend from higher to lower correlations

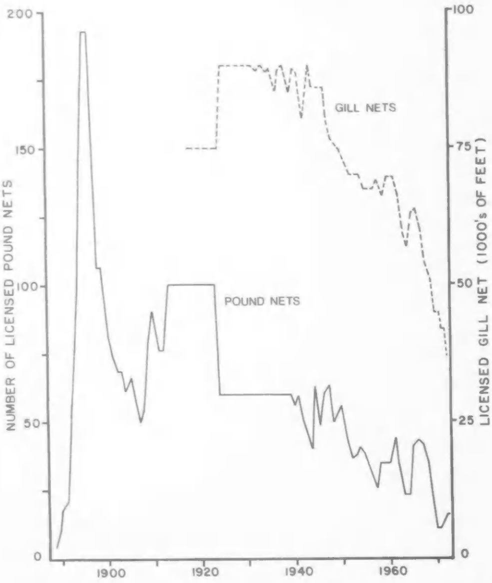

FIG. 3. Trends in commercial fishing gear licensed for Minnesota waters of Lake of the Woods, 1888–1973.

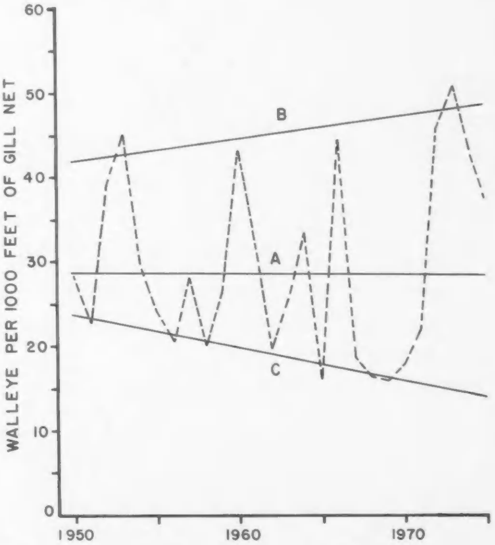

FIG. 4. Catches of walleye/1000 ft of commercial gill net, Lake of the Woods, Minnesota, 1949–1975, and linear regressions of CPE on time for all years (*A*), four high values (*B*), and six low values (*C*). $b_A = -0.011$, $b_B = 0.279$, $b_C = -0.388$; $r_A = -0.007$, $r_B = 0.700$ ($P < .35$), $r_C = -0.964$ ($P < .01$).

between walleye yields and total yields in the later years was similar to those observed for sturgeon and whitefish in the early years of the fisheries. Precipitous reductions in yield of sturgeon and whitefish were associated with the reduced correlations. In contrast, correlations between yields of lesser-valued species ("other" in Table 2) and total yields increased.

Analysis of data on gillnet catches and effort for Minnesota from 1949 to 1973 also suggests that exploitation may have contributed to changes in abundance and recruitment of walleye. A linear multiple regression of commercial walleye yield on effort and CPE for these years indicated that 41.6% ($r = 0.645$, $P < 0.01$) of the variation in walleye yield was attributable to changes in fishing effort and 54.9% to CPE ($r = 0.823$, $P < 0.01$). The correlation between gillnet effort and CPE was positive ($r = 0.14$), but not significant. The high proportion of variation accounted for by changes in CPE and the significant decline in total yield noted earlier suggest that the abundance of commercially legal walleyes in Minnesota waters declined from 1949 to 1973.

Recruitment of commercially legal walleye appeared to fluctuate more widely in recent years. Linear regressions of CPE on time for all years from 1949 through 1973 (Fig. 4) indicated no change in trend of CPE. But the slope for the four high CPE values diverged from that for the six low CPE values. These diverging slopes suggest that walleye abundance in the Minnesota waters was oscillating with increasing amplitude. The lowest and highest values of CPE in the 25-yr series occurred within a 5-yr period, in 1969 and 1973, respectively.

Warnings by Regier et al. (1969) concerning the sudden appearance of a large year-class of a valued species and intensive fishing of an oscillating population appear pertinent to the Minnesota waters. A huge year-class of walleye was produced in the Big Traverse in 1966. This year-class made up 64% of experimental gillnet catches at age II, 83% at age III, and 79% at age IV (Schupp 1974). The commercial harvest of 37,000 kg in 1969 was the lowest recorded. The 1966 year-class began recruiting to the commercial fishery in 1971, and in 1973 the commercial harvest was nearly four times as great as in 1969 and CPE was the highest on record.

Commercial production of walleye from Ontario, though less variable than Minnesota's, also fluctuated more widely since 1950. The highest yields recorded were in 1961 and 1962, and the lowest yield since 1920 occurred in 1970.

The effect of the Shoal Lake commercial fishery on production from Ontario waters during this period was noted earlier. Shoal Lake has an area of 25,900 ha and, on the basis of the MEI (Ryder 1965), the theoretical yield is 5.0 kg·ha^{-1} per year. In contrast, the commercial harvest averaged 7.0 kg·ha^{-1} annually from 1959 to 1968 (Table 3). The commercial walleye harvest from Shoal Lake also appeared to be excessive in that period. The annual yield averaged 4.3 kg·ha^{-1} from 1959 through 1963, in contrast to the 1956–75 average of 1.9 kg·ha^{-1}. These high yields were enough to account for the interrupted downtrend and contributed substantially to the record walleye yields in 1961 and 1962. Growth rates for 3–6-yr-old walleye increased during this period (unpublished data).

Based on data from a series of 70 Ontario lakes, Adams and Olver (1977) suggested that a percid harvest approximating one-third of the total harvest may be an emergent property of Boreal percid fisheries. If the theoretical yield is proportioned on this basis, percid yields of 1.26 and 1.7 kg·ha^{-1} annually are indicated for Ontario and Minnesota, respectively. The commercial walleye yield from Ontario exceeded 1.26 kg·ha^{-1} twice before 1930, each year from 1933 through 1936, and 5 years during 1936–73 including 3 years of high production from Shoal Lake (1960–62). Walleye made up 44.7% of the total yield during 1933–36 and 63.9% of the Shoal Lake yield for 1960 through 1962. Commercial walleye yields from Minnesota exceeded 1.7 kg·ha^{-1} each year during 1923–37 and in only 3 years during 1937–73. Annual yields of percids from Minnesota averaged 4.5 kg·ha^{-1} from 1933 through 1937; walleye yields alone averaged 2.9 kg·ha^{-1}. Of the total harvest during these 5 years 61.8% was contributed by percids.

TABLE 3. Annual commercial harvests (kg·ha^{-1}) of walleye and of all species from Shoal Lake, Ontario, 1956–75.

Year	Walleye	All species
1956	1.1	5.0
1957	1.5	4.9
1958	2.2	5.1
1959	3.1	5.7
1960	4.0	6.0
1961	5.6	8.3
1962	4.9	8.4
1963	3.7	8.6
1964	2.6	8.0
1965	1.5	7.3
1966	1.5	6.0
1967	2.6	6.5
1968	3.9	8.5
1969	1.6	4.7
1970	1.1	4.3
1971	2.2	5.4
1972	1.7	4.6
1973	1.5	5.7
1974	0.5	3.9
1975	1.3	4.5

But the decline in walleye production cannot be attributed entirely to the effects of commercial fishing. The creel surveys suggest that sportfishing was at least as important. It was estimated that the sportfishing harvest in Ontario exceeded the commercial harvest by 1940 (unpublished data). The combined commercial and sportfishing harvests averaged 1.2 kg·ha^{-1} from Minnesota waters for 1968–70 of which the sport fishery harvested 73%.

Sportfishing harvested younger and smaller walleye than the commercial fishery. Female walleye were recruited to the commercial fishery in 1968–70 mainly at age V and males at age VI (Heyerdahl and Smith 1972). Age-classes V–VII contributed 83.9% of the commercial gillnet catch. The sportfishing harvest was primarily from age-classes III–VI (Schupp 1974). The walleye harvest from the Minnesota sport fishery consisted of 45% of fish less than age V in contrast to less than 5% for the gillnet fishery. The 1963 year-class was the greatest contributor to the sport and commercial fisheries in Minnesota during 1968–70. It yielded 1.7 kg·ha^{-1} to the combined fishery for these years, 69.6% of which was taken by the sport fishery. The sport fishery harvested 0.8 kg·ha^{-1} from the year-class at age V compared with a commercial harvest of 0.5 kg·ha^{-1} summed over ages V–VII. The 1966 year-class was readily accepted by anglers at 300 mm TL, nearly 100 mm shorter than the legal commercial length (Schupp 1974; Heyerdahl and Smith 1972).

Sauger

The Big Traverse of Lake of the Woods is typical of the habitat preferred by sauger (Scott and Crossman 1973). It is large, shallow, and turbid. Various studies have indicated that sauger are numerically four to six times as abundant as walleye in the southern portions of the lake (Heyerdahl and Smith 1972; Scidmore 1963; Schupp 1974).

No long-term trends in sauger yields were evident. Excepting the years 1931–37, the annual commercial yield from 1926 to 1973 averaged 0.2 kg·ha^{-1} ranging from 0.05 to 0.5. Commercial production from Minnesota averaged 1 kg·ha^{-1} from 1931 through 1937 due to increased use of small-mesh gill nets. Yields from

TABLE 4. Mean annual yields ($kg \cdot ha^{-1}$) and percentages of the total harvest from the two waters of various species from Ontario and Minnesota waters of Lake of the Woods (1952–73).

	Ontario		Minnesota	
Species	Yield	% of total	Yield	% of total
Sturgeon	tr	100.0	0.00	0.0
Lake trout	0.01	100.0	0.00	0.0
Cisco	0.26	11.8	3.60	88.2
Lake whitefish	0.20	99.7	tr	0.3
Northern pike	0.60	84.5	0.20	15.5
White sucker	0.54	71.1	0.41	28.9
Bullhead	0.11	86.3	0.03	13.7
Burbot	0.35	33.9	1.68	66.1
Black crappie	0.04	100.0	0.00	0.0
Yellow perch	0.02	6.3	0.59	93.7
Sauger	0.05	30.5	0.22	69.5
Walleye	0.98	70.9	0.75	29.1
All species	3.16	47.4	7.48	52.6

southern areas in Ontario were similar to those from Minnesota, but yields from northern areas were 0.05 $kg \cdot ha^{-1} \cdot yr^{-1}$ from 1952 to 1973 ranging from 0.01 to 0.09. The Minnesota fishery accounted for 69.5% of the total harvest from 1952 to 1973 (Table 4).

The average harvest of sauger by the sportfishery in the Minnesota waters during 1968–70 was 0.1 $kg \cdot ha^{-1}$ (Schupp 1974). The combined sport and commercial harvest during these years was below the long-term average commercial production, reflecting the relatively low abundance of sauger at that time.

The commercial harvest records suggest that abundance of sauger fluctuates widely and these fluctuations appear to be independent of fishing. Although sauger yields from the Minnesota waters were lower than the long-term mean, growth rate was lower and annual mortality was less than 30 yr ago (Heyerdahl and Smith 1972).

Sauger have increased in abundance recently in northern areas of the lake and a few have been reported in commercial catches from Shoal Lake for the first time (unpublished data). This may be a response to increasing turbidity.

Yellow Perch

Yellow perch are an important component of the Lake of the Woods fish community but have been relatively unimportant to sport and commercial fisheries. Mean annual commercial harvest from 1952 to 1973 was 15,000 kg, about 60% from Minnesota. The commercial production of perch averaged less than 0.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the southern areas of the lake and a fraction of that in the northern areas. Production has been stable for the last 40 yr. Minnesota creel surveys indicated that anglers harvested an average of 4,100 $kg \cdot yr^{-1}$ from 1968 to 1970, about 40% of the commercial production in those years.

Industrial Pollution

The loss of river spawning areas through pollution of the Rainy River by the paper industry may have affected the Lake of the Woods fish community. The decline of lake sturgeon occurred before destruction of the spawning sites in the river, but the loss of these areas probably contributed to the later stages of the decline (Carlander 1949). Longnose sucker (*Catostomus catostomus*) and lake whitefish may also have spawned in the Rainy River. Longnose suckers were not observed in the most recent investigations on the Big Traverse and whitefish were uncommon.

Pollution by papermill wastes discharged into the Rainy River may also have been detrimental to percids. The slime bacterium *Sphaerotilus natans*, associated with these wastes, adversely affected walleye egg and fry survival by preventing free water circulation around the eggs and by entangling newly hatched fry (Smith and Kramer 1963). Sulfide concentrations associated with deposits of the wastes in the river were high enough to account for egg and fry mortalities (Colby and Smith 1967). Low concentrations of dissolved oxygen and high concentrations of carbon dioxide at and above the wood fiber/sludge substrate may also have affected walleye adversely. Any influence the pollution may have had on percid reproduction in the Rainy River was not reflected in yields from the lake.

Discussion

Exploitation appears to be the only cultural source of stress that may have affected Lake of the Woods percids markedly. On the basis of guidelines suggested by Adams and Olver (1977), the harvest of percids, especially walleye, was excessive in the 1930s. The long-term decline in commercial walleye yields began after these high harvests. Recent estimates of the combined sport and commercial yields approximate the commercial yield of the 1930s.

The evidence for adverse effects of exploitation on the walleye stocks is not conclusive, but we consider the arguments that fishing has had an adverse effect are substantial. The stocks could probably have maintained the yields for commercial or sport fisheries alone, but dual exploitation was probably the main cause of the recent unstable yields. Continued intensive harvest would most likely intensify the fluctuations in yield.

Current management policy in Ontario and Minnesota recognizes the desirability of coexisting commercial and sport fisheries. Commercial fishing is the only economical way to harvest species of fish not taken by anglers. Sportfishing interests are, however, usually opposed to commercial fishing and have successfully resisted efforts to change fishing practices that might have benefitted both factions while reducing conflicts between them. Efforts to introduce commercial trawls as a subsitute for existing gear in Minnesota failed, though the substitution would have reduced commercial walleye yields to low levels while continuing to harvest nongame species (Scidmore 1963; Heyerdahl and Smith 1972).

Ontario has a viable commercial fishery of widely scattered, small gillnetting operations. Management policy is to encourage continuation of this fishery, but more stringent regulation is envisioned. Large areas of the lake are closed to commercial fishing and in other portions only restricted netting is allowed (Fig. 1). These are areas where angling pressure is greatest or productive potential is least. Harvest quotas for walleye are being considered in areas still open to unrestricted commercial fishing. This appears to be the only practical means of conserving walleye stocks where exploitation is intense.

The increasing turbidity of waters in the northern areas in Ontario and the concomitant spread of the less-desirable sauger are also of concern. Fishing practices and regulations are such that the small, slow-growing sauger would probably be underharvested.

The rate of attrition on gill netters in Minnesota has increased rapidly and it is likely that gill nets will be eliminated within 20 yr. The licensing of entrapment gears (pound nets, fyke nets, and submarine trap nets) is authorized, but there has been relatively little interest in these.

The elimination of commercial fishing does not appear to be desirable. Cisco, white sucker, and burbot are abundant and can sustain a substantial harvest. The relative lack of sportfishing interest in sauger and yellow perch would also permit a commercial harvest. The long-term commercial catch of walleye is about 10 times that of sauger though sauger are numerically more abundant. Continued selective fishing pressure on walleye in the absence of a significant harvest of other species may be an ultimate detriment to the stocks of walleye.

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Year-Class Abundance, Population, and Production of Walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with Varied Fry Stocking Rates[1,2]

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CARLANDER, K. D. AND P. M. PAYNE. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34: 1792–1799.

Year-class abundance of walleye, *Stizostedion vitreum vitreum*, in Clear Lake from 1948 to 1974 was significantly correlated ($r = 0.613$) with annual fry stocking, which was varied from 0 to 6070 fry/ha. Abundance of young walleye seined along shore was even more highly correlated with fry stocking ($r = 0.819$) but not significantly correlated with year-class abundance ($r = 0.179$) indicating that year-class strength may change between the first summer and later years. No correlation was found between year-class abundance and temperature in summed degree-days, water levels, or abundance of yellow perch, *Perca flavescens*, as effects were probably masked by the fry stocking. Growth of age 0 and I walleye were negatively correlated with fry stocking ($r = -0.42$ and $r = -0.41$, respectively), but growth of age V walleye was positively correlated ($r = 0.70$). Growth was also correlated with water levels ($r = 0.79$). Annual mortality rate averaged 42%. Standing crop ranged from 2.63 to 16.52 kg/ha and annual production from 1.01 to 9.31 kg/ha. Production per biomass was low when water levels were low.

Key words: Percidae, walleye, *Stizostedion vitreum vitreum*, population dynamics, productions, Clear Lake, Iowa, stocking

CARLANDER, K. D., AND P. M. PAYNE. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34: 1792–1799.

Il existe une corrélation significative ($r = 0.613$) entre l'abondance des classes d'âge du doré jaune, *Stizostedion vitreum vitreum*, dans le lac Clear, de 1948 à 1974 et les peuplements annuels d'alevins, variant de 0 à 6070 alevins/ha. L'abondance des jeunes dorés jaunes capturés à la senne le long du rivage est encore plus étroitement liée aux peuplements d'alevins ($r = 0.819$), mais il n'y a pas de corrélation significative avec l'abondance des classes d'âge ($r = 0.179$), ce qui indique que l'abondance des classes d'âge peut changer entre le premier été et les années subséquentes. Nous n'avons pas trouvé de corrélation entre l'abondance des classes d'âge et la température comme somme de degrés-jours, les niveaux d'eau ou l'abondance de la perchaude, *Perca flavescens*, étant donné que les effets sont probablement masqués par les peuplements d'alevins. La croissance des dorés jaunes d'âges 0 et 1 montre une corrélation négative avec les peuplements d'alevins ($r = -0.42$ et $r = -0.41$, respectivement), mais la corrélation est positive pour les dorés jaunes d'âge V ($r = 0.70$). La croissance est également liée aux niveaux d'eau ($r = 0.79$). Le taux de mortalité annuelle est de 42% en moyenne. La biomasse varie de 2.63 à 16.52 kg/ha, et la production annuelle de 1.01 à 9.31 kg/ha. La production par biomasse est faible quand les niveaux d'eau sont bas.

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FISH populations have been monitored at Clear Lake, Iowa, since 1942. In this paper, we relate the annual stocking of walleye, *Stizostedion vitreum vitreum* (Mitchill), fry to abundance of year-classes and estimate annual biomass and production of walleye. Numbers of walleye fry stocked from 1948 to 1972 were varied (Table 1) to evaluate the effect of stocking. An earlier report on the results of the 1948–57 stocking (Carlander et al. 1960) showed that walleye from years when fry were stocked were more abundant than in years dependent only upon natural spawning, but questions were raised about the effect of the regular alternation in stocking. The 1961–72 stocking rates were thus varied

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Journal paper J-8617 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa.

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TABLE 1. Numbers of walleye fry stocked per hectare, mean catches of walleye per gillnet-hour (C/f), year-class abundance indexes, and numbers of young-of-the-year walleye and yellow perch caught per standardized seine haul by calendar year.

				Young-of-the-year	
Year-class	Fry stocked	C/f[a]	Year-class abundance[b]	Walleye	Yellow perch
1948	3870	0.180	1.44	—	—
1949	0	0.540	0.74	—	—
1950	3580	0.750	3.08	—	—
1951	0	0.200	0.67	—	—
1952	2205	0.460	2.82	—	—
1953	0	0.470	0.24	—	—
1954	2833	0.530	0.83	—	—
1955	0	0.498	0.13	—	—
1956	2860	0.215	0.17	22.75	8.47
1957	0	0.280	0.18	0.58	3.57
1958	2934	0.186	0.23	12.33	0.22
1959	—	0.236	0.26	6.00	5.92
1960	2152	0.104	0.29	19.66	0.20
1961	405	0.145	0.10	1.37	1.32
1962	202	0.156	0.13	0.25	0.16
1963	6070	0.036	1.50	—	—
1964	4047	0.097	1.39	—	—
1965	2024	0.318	0.75	3.00	2.65
1966	2024	0.287	1.21	20.66	6.90
1967	1012	0.352	0.67	2.44	2.07
1968	4047	0.471	1.43	9.11	2.93
1969	202	0.253	0.63	3.33	1.06
1970	405	0.256	0.40	1.77	0.83
1971	1012	0.184	0.55	4.66	1.08
1972	6070	0.129	10.21	32.33	6.35
1973	—	0.747			
1974	—	0.870			

[a] Data from Iowa Cooperative Fishery Research Unit Quarterly Reports. 1957–61 C/f values were reduced 8% to adjust for reduced water area those years.

[b] The mean C/f each year was multiplied by the percentages of the catch in ages I, II, and III. Individual C/f values in each age-group I–III were divided by the mean of that age-group (4.114, 9.403, and 7.590, respectively). The year-class abundance index is the mean of the adjusted C/f for the three age-classes representing that year-class.

according to an irregular pattern. The fry came from walleye gillnetted from spawning areas in the lake.

Clear Lake (44°N and 94°W) is a 1474-ha eutrophic lake (Table 2), and represents the original southern limit of walleye in lakes. Water levels were below the outlet from 1955 to 1960 (Fig. 1) and the area of the lake was reduced about 8% when the water was lowest, 1 m down (McCann and Carlander 1970). Bailey and Harrison (1945) listed 43 species of fish from the lake. The walleye is the most abundant predator species.

General Methods

Graduate students from the Iowa Cooperative Fishery Research Unit collected scale samples and catch data each summer from 1947 to 1974 with a variety of gear. Gillnet sampling from 1947 to 1952 was concentrated in one area (Carlander 1954) but by 1958 it was standardized to include the entire lake (Bulkley 1970a). Gillnet catches showed a diel cycle (Carlander 1954) and were adjusted to represent equal sampling throughout the 24 h.

Ages and growth of walleye were determined from scale examination and measurement (Cleary 1949; Carlander and Whitney 1961).

Relation Between Fry Stocking and Year-Class Abundance

Abundance indexes for year-classes 1948–72 (Table 1) were highly correlated with the number of fry stocked ($r = 0.613$, df 22). If the very abundant 1972 year-class is eliminated, the correlation is still significant ($r = 0.563$, df 21).

TABLE 2. Physical and chemical characteristics of Clear Lake, Iowa.[a]

Physical		
Lake area	(ha)	1747
Watershed area	(ha)	3400
Mean depth	(m)	3.6
Maximum depth	(m)	6
Shoreline development factor		1.58
Littoral zone (<2m)		25%
Little overflow most years		
Not thermally stratified in summer		
Chemical (as ppm)		
Total alkalinity		143
Total dissolved solids		230
Calcium		23
Magnesium		22
Sulfate		13
Chloride		7.8
Nitrite nitrogen		0.004
Phosphate		0.002
Other		
Transparency (summer mean, m)		1.4
Specific conductivity (microhms)		306
pH		8.6
Morphoedaphic index (metric)		64

[a] The chemical data are mostly from Bachmann (1967) and the physical data from Pearcy (1953). The nitrogen, phosphate, and pH data came from Bailey and Harrison (1945). The total dissolved solids were reported by the State Hygienic Laboratory, Iowa City.

During the low water years 1956–61, year-class strength was poor. Elimination of these year-classes improved the correlation with fry stocking ($r = 0.641$, df 17).

Numbers of age 0 walleye collected in a 9.1-m bag seine (7-mm mesh) from 1956 to 1972 (Table 1) were also highly correlated with the number of fry stocked ($r = 0.819$, df 13). Correlation between numbers of age 0 walleye and year-class abundance indexes (excluding the very abundant 1972 year-class) was only 0.179, indicating that year-class strength may change between the middle of the first summer and ages I to III.

Year-Class Abundance and Other Factors

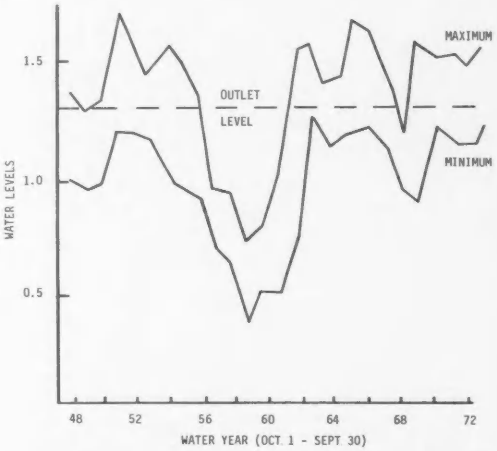

FIG. 1. Maximum and minimum water levels (m) at Clear Lake, Iowa, 1948–72.

Success of walleye year-classes in western Lake Erie has been shown to be affected by water temperatures during spring spawning and incubation (Busch et al. 1975). However, time of ice-out, the rate of warming, total number of degree-days above 5.5°C (Ryder 1972), and the duration of ice cover the next winter after spawning showed no significant correlation with year-class abundance in Clear Lake. Although year-class abundance was low during drought years (1956–62), water levels were not significantly correlated with year-class abundance.

Success of walleye year-classes has been correlated with success of yellow perch, *Perca flavescens* (Mitchill), reproduction in two Minnesota lakes (Maloney and Johnson 1957), and in Lake Oneida (Forney and Noble 1970). Numbers of young walleye and yellow perch (Table 1) were significantly correlated in Clear Lake, 1956–72 ($r = 0.606$, df 13). Excluding 1972, the relationship is still significant ($r = 0.532$, df 12). Yellow bass, *Morone mississippiensis* Jordan and Eigenmann, were a more abundant prey for walleye than were perch from 1947 to 1968. Almost complete elimination of yellow bass in 1968 by an *Aeromonas salmonicida* infection (Bulkley 1970b) was followed by an increase in abundance and average size of yellow perch. Walleye fry in Clear Lake begin feeding on larval fish at approximately 31 mm in length (Bulkley et al. 1976). Yellow perch fry usually are available at this critical time whereas yellow bass fry do not emerge until considerably later.

The effects of fry stocking probably masked effects of climate or other factors. A step-down multiple regression analysis of year-class abundance to (1) number of fry, (2) C/f of yellow perch, (3) number of degree-days above 5.5°C, and (4) mean water levels failed to show any significance (at $P = 0.05$) except for fry stocking. Yellow perch C/f, however, approached significance ($r = 0.30$, $P < 0.10$) when the effects of fry stocking were removed.

TABLE 3. Mean calculated total lengths (mm) of walleyes at each annulus by year-classes, 1948–72.

Year-class	Numbers in samples per age-group[a]	Length at each annulus												
		1	2	3	4	5	6	7	8	9	10	11	12	13
1948	73, 116, 16, 28, 8, 4, 4, 1, 2, 1; 0, 1	166	298	384	436	479	573	551	606	618	659	655	670	
1949	16, 61, 69, 28, 5, 1, 2, 3; 0, 2, 2, 3, 4	176	264	349	434	493	533	553	577	604	605	605	625	640
1950	103, 340, 129, 40, 19, 17, 26, 4; 4, 9, 7, 1	171	265	363	442	487	520	546	576	576	606	607	609	
1951	49, 15, 13, 12, 15, 19, 1; 12, 6, 7, 0, 1	197	297	379	435	480	507	545	557	596	636	648	660	
1952	21, 82, 110, 41, 58, 7; 17, 8, 20, 5, 1	189	290	374	425	465	504	527	558	571	581	602		
1953	1, 8, 14, 21, 8; 22, 14, 15, 5	186	289	378	427	468	496	514	548	490				
1954	16, 38, 33, 7; 21, 10, 20, 7, 2, 0, 3	186	303	382	428	449	470	482	533	554	586	594		
1955	6, 4, 1; 13, 8, 16, 4, 2, 0, 3, 1	188	285	386	431	464	485	540	566	627	640	648		
1956	5, 2; 6, 2, 7, 7, 2, 0, 3	184	286	376	430	469	478	535	619	642				
1957	3; 9, 2, 2, 8, 4, 0, 2, 2	190	287	354	394	429	486	520	539	561				
1958	3, 3, 53, 26, 10, 0, 5, 8, 2, 0, 1	169	251	344	401	489	532	562	578	581	607	615		
1959	4, 27, 16, 4, 0, 10, 5, 2, 1, 1, 1	175	265	336	411	477	512	551	588	619	640	653		
1960	62, 49, 57, 0, 29, 14, 1, 7, 2, 1	172	263	332	416	472	486	534	559	638	668			
1961	14, 61, 0, 52, 42, 15, 10, 3	175	258	346	412	458	488	520	602					
1962	21, 0, 21, 20, 8, 9, 2, 0, 1	172	267	344	407	436	452	500	518	581				
1963	0, 141, 68, 22, 22, 2, 1, 2	185	273	341	386	438	530	554	578					
1964	62, 116, 50, 32, 6, 6, 7	176	263	344	404	480	509	555						
1965	56, 37, 14, 3, 7, 2, 1, 1	169	275	338	412	455	535	554	617					
1966	30, 72, 6, 25, 9, 1, 1, 3	163	249	304	377	454	522	565	584					
1967	16, 68, 42, 33, 2, 2	172	258	338	395	425	442							
1968	57, 95, 47, 7, 18, 3	169	260	321	381	427	498							
1969	27, 52, 15, 24, 1	176	260	352	427	472								
1970	4, 22, 15, 6	191	261	338	469									
1971	12, 28, 3	187	272	340										
1972	170, 185	163	256											

[a] The data on age-groups collected through 1958 are from Carlander and Whitney (1961) and are separated by semicolons from the data calculated by Payne.

TABLE 4. Instantaneous growth rates[a] in weight of walleye by age-group in Clear Lake, 1948–73.

Year	I	II	III	IV	V
1948	1.619	0.774	0.398	0.248	0.184
1949	1.636	0.858	0.363	0.276	0.143
1950	1.299	0.697	0.367	0.214	0.152
1951	1.361	0.919	0.408	0.206	0.191
1952	1.330	0.988	0.569	0.260	0.162
1953	1.382	0.832	0.483	0.259	0.189
1954	1.411	0.886	0.510	0.248	0.220
1955	1.483	0.842	0.396	0.302	0.238
1956	1.565	0.747	0.401	0.246	0.165
1957	1.376	0.760	0.350	0.232	0.160
1958	1.314	0.783	0.396	0.218	0.169
1959	1.219	0.752	0.308	0.225	0.164
1960	1.336	0.979	0.575	0.179	0.139
1961	1.286	0.734	0.602	0.263	0.155
1962	1.249	0.671	0.552	0.376	0.167
1963	1.269	0.885	0.543	0.304	0.278
1964	1.099	0.782	0.547	0.398	0.236
1965	1.217	0.726	0.549	0.318	0.170
1966	1.404	0.807	0.563	0.416	0.194
1967	1.386	0.720	0.389	0.286	0.128
1968	1.256	1.062	0.467	0.266	0.279
1969	1.412	0.764	0.370	0.260	0.152
1970	1.645	0.676	0.521	0.268	0.151
1971	0.944	0.696	0.431	0.278	0.195
1972	1.019	0.696	0.425	0.286	0.154
1973	1.415	0.890	0.687	0.249	0.169

[a] In calculating instantaneous growth, G, only the fish which completed the year's growth were used. e.g. Age I fish were not used in calculating the mean length at the first annulus in determining the increment in the second year. The mean lengths were converted to weights and $G = \log_e W_{n+1} - \log_e W_n$.

TABLE 5. Catches per gillnet-hour and population estimates of walleye in Clear Lake 1948–74.

Year	C/f	Walleyes over 305 mm		Population estimates		
		%	C/f	Over 305 mm[a]	All sizes	Rounded by 3's
1948	0.180	68	0.122	8576	12612	24783
1949	0.540	85	0.459	31411	36954	33561
1950	0.750	93	0.697	47538	51116	34085
1951	0.200	49	0.098	6950	14184	32294
1952	0.460	75	0.345	23687	31583	25992
1953	0.470	91	0.428	29311	32210	33324
1954	0.530	96	0.509	34731	36178	34154
1955	0.498	90	0.408	30666	34073	28380
1956	0.215	94	0.202	13997	14890	22757
1957	0.280	96	0.269	18537	19309	15715
1958	0.186	94	0.175	12168	12945	16190
1959	0.236	97	0.229	15827	16316	12229
1960	0.104	89	0.093	6611	7425	11357
1961	0.145	64	0.093	6611	10330	9596
1962	0.156	63	0.098	6950	11032	8136
1963	0.036	48	0.017	1462	3046	8872
1964	0.097	—	—	—	—	12538
1965	0.318	62	0.197	13658	22029	18199
1966	0.287	55	0.158	11016	20029	22129
1967	0.352	67	0.236	16301	24330	25618
1968	0.471	56	0.264	18198	32496	24938
1969	0.253	36	0.091	6476	17989	22784
1970	0.256	59	0.151	10541	17866	16228
1971	0.184	79	0.145	10135	12824	13324
1972	0.129	53	0.068	4917	9277	24533
1973	0.747	36	0.269	18537	51492	41039
1974	0.870	11	0.096	6815	61955	61955

[a] Derived from the regression of C/f on five mark-and-recapture estimates, given in the text.

Growth

The calculated growth rates for the various year-classes of Clear Lake walleye (Carlander and Whitney 1961) showed a negative correlation with year-class abundance for the years 1935–57. Such a correlation supports the evidence that, for fish in general, growth rate usually decreases as population density increases. Lengths calculated from scale measurements at each annulus (Table 3) were converted to weights using a weight–length regression based on 489 Clear Lake walleye collected in 1961–62 (Sriprasert 1974):

$$\log W = -5.4187 + 3.1413 \log L.$$

This procedure involved an underestimate of weight, and of the subsequent biomass estimates, "commonly in the order of 5%" (Ricker 1975, p. 211).

Negative correlations were found between numbers of fry stocked and instantaneous growth (Table 4) in the first ($r = -0.42$, $P < .05$) and second ($r = -9.41$, $P < .056$ years of life. This may have been related to increased density. The growth of age V walleye was positively correlated ($r = 0.70$, $P < .008$) with fry stocking. Chevalier (1973) stated that predation by age III and older (III+) walleyes was the most probable cause of mortality of young walleye in late summer and fall in Lake Oneida. A similar predation at Clear Lake may have resulted in an increased growth of older walleyes correlated with the numbers of fry stocked.

Carlander and Whitney (1961) reported a significant correlation ($r = 0.565$, df $= 21$) between summer temperatures and growth in Clear Lake for 1935–57; however, no correlation between temperature, in summed degree-days, and the average instantaneous growth rate was found for 1948–73. Instantaneous growth was significantly correlated with water levels ($r = 0.79$, $P < .0001$).

TABLE 6. Mark-and-recapture population estimates of adult walleye in Clear Lake and associated catch-per-effect for certain years.

Source	Year of estimate	Walleye over 305 mm	
		Number[a]	C/f[a]
Whitney (1958)	1953	30,822	0.428
McCann and Carlander (1970)	1958	11,800	0.175
	1959	12,300	0.229
Hollingsworth (1967)	1966	11,716	0.158
Schutte, S., I.S.C.C. Personal communication	1972	6,600	0.068

[a] Except for 1953, the numbers are means of 2 to 4 estimates derived from the data by various modifications. Variation between the estimates was small within each year.

[b] Values (C/f) from Table 5.

TABLE 7. Population estimates of walleye by age-groups each year based on numbers at age III computed from the regressions of the year classes and assuming an annual mortality of 42%.

Year	I	II	III	IV	V	VI	Total[a]
1948	24831	15121	4063	1935	831	462	48689
1949	10767	14402	8770	2357	1122	482	38647
1950	14138	6245	8353	5087	1367	651	36554
1951	46671	8200	3622	4845	2950	793	67781
1952	10648	27069	4756	2101	2810	1711	49950
1953	40678	6176	15700	2758	1218	1630	69653
1954	7803	23593	3582	4106	1600	707	48203
1955	11558	4526	13684	2078	5281	928	39515
1956	11008	6703	2625	7937	1205	3063	33926
1957	1650	6384	3888	1523	4603	699	21325
1958	1653	957	3703	2255	883	2670	14019
1959	6683	959	555	2148	1308	512	14821
1960	3098	3876	556	322	1246	759	11691
1961	3668	1797	2248	322	187	723	10530
1962	4703	2128	1042	1304	187	108	10763
1963	4257	2728	1234	604	766	108	10525
1964	19290	2469	1582	716	351	439	25390
1965	16843	11188	1432	918	415	203	31556
1966	5016	9769	6489	830	532	241	23332
1967	8038	2909	5666	3764	482	309	21564
1968	12970	4662	1687	3286	2183	279	24583
1969	13769	7522	2704	978	1906	1266	28542
1970	14524	7986	4363	1568	568	1106	31077
1971	10181	8424	4632	2473	910	329	28147
1972	3523	5905	4886	2687	1434	528	19848
1973	98274	2043	3425	2834	1558	832	109783
1974		56999	1185	1987	1644	904	63201

[a] The totals for 1948 to 1960 include average numbers for the 1941 and earlier year-classes. The addition was 1135 to the 1948 collection and 42% less in each successive year.

Standing Crop and Production of Walleye

To estimate annual biomass and production, C/f values were converted to population numbers (Table 5) by using mark and recapture estimates made in five of the years (Table 6). A correlation between these population estimates, Y, and adjusted C/f values, X, was significant ($r = 0.974$, df $= 3$) and the regression was

$$Y = 310 + 67759\,X.$$

Since most of the population in a given year must have been present the previous and following years, estimates were averaged by three's to reduce some of the irregularities. Population estimates were proportioned to age-groups on the basis of scale samples each year. Regressions of logarithms of numbers in each age-group (beginning with the most numerous age-group) within a year-class gave estimates of mortality rates (Ricker 1975) which ranged from 22 to 63% and averaged 42.5%. The combined data in one regression gave a mortality rate of 42%.

Numbers of age III walleye in each year-class were computed from the regression lines and the average mortality rate of 42% was applied to estimate numbers in each age-group (Table 7). Age III was selected since the average age of fish used in the regression was 3.2 yr. The numbers in each age-group were then converted to biomass by multiplying by the mean weight.

Standing crop ranged from 16.52 kg/ha in 1954 to 2.63 kg/ha in 1963 (Table 8). Even the peak standing crop of age III±, 11.30 kg/ha, was below the mean of 16 kg/ha for lakes summarized by Carlander (1977). The mean age II± standing crop was also below the lowest reported for those lakes, 6.1 kg/ha for West Blue Lake, Manitoba (Kelso and Ward 1972).

The morphoedaphic index for the lake is 64, in comparison with 40 for the optimum (Ryder et al. 1974) which indicates a more eutrophic condition than optimum. The number of competing species of fish in Clear Lake may be related to the low standing crop of walleye.

Annual production was estimated by multiplying the instantaneous growth rate by the mean biomass (i.e. the mean of the biomass at the

TABLE 8. Standing crops and annual production (kg/ha) of walleye in Clear Lake, 1948–74

	Standing crop		Annual Production		
Year	III+	I+	III+	I+	0+
1948	4.90	7.90	1.00	4.15	4.53
1949	6.06	8.35	1.51	4.62	5.38
1950	8.36	9.73	1.89	3.48	3.74
1951	8.30	10.39	1.63	5.36	5.77
1952	8.13	11.44	1.65	6.19	7.42
1953	9.99	12.42	3.07	7.26	9.31
1954	9.98	16.52	2.14	6.14	7.63
1955	11.30	12.33	2.91	4.64	4.91
1956	10.56	12.16	1.76	3.62	4.02
1957	8.90	9.88	1.34	2.28	2.68
1958	7.90	8.11	1.27	1.52	1.58
1959	5.70	6.03	0.72	1.14	1.20
1960	4.12	4.59	0.49	1.09	1.26
1961	3.42	3.74	0.59	0.95	1.04
1962	2.50	2.86	0.50	0.91	1.01
1963	2.25	2.63	0.46	0.99	1.12
1964	2.09	3.02	0.48	1.79	1.91
1965	1.88	3.67	0.42	2.35	3.00
1966	2.90	4.04	1.04	2.33	2.82
1967	3.63	4.16	0.97	1.64	1.77
1968	3.45	4.21	0.93	2.06	2.25
1969	3.86	4.95	0.64	2.16	2.51
1970	3.73	5.02	0.93	2.68	3.03
1971	3.94	5.30	0.88	2.13	2.55
1972	4.32	5.04	1.04	1.70	2.09
1973	4.27	6.77	1.32	6.98	6.98
1974	4.40	9.82	—	—	—
Mean without 1972 year-class	5.72	7.23	1.21	2.87	3.31
			with 1972	3.08	3.53

TABLE 9. Annual production per biomass at beginning of season (P/B_o ratios) and per mean biomass[a] ($P/\bar{B}$ ratios) for walleye in Clear Lake, 1948–73.

	P/B_o		$P/\bar{B}$	
Year	III+	I+	III+	I+
1948	0.20	0.53	0.24	0.52
1949	0.25	0.55	0.26	0.52
1950	0.23	0.36	0.24	0.37
1951	0.20	0.52	0.21	0.50
1952	0.20	0.54	0.24	0.55
1953	0.31	0.58	0.33	0.51
1954	0.21	0.37	0.25	0.43
1955	0.26	0.38	0.28	0.39
1956	0.17	0.30	0.19	0.33
1957	0.15	0.23	0.17	0.25
1958	0.16	0.19	0.19	0.22
1959	0.13	0.19	0.15	0.22
1960	0.12	0.24	0.14	0.26
1961	0.17	0.25	0.21	0.29
1962	0.20	0.32	0.22	0.34
1963	0.20	0.38	0.23	0.40
1964	0.23	0.59	0.26	0.56
1965	0.22	0.64	0.26	0.62
1966	0.36	0.58	0.40	0.58
1967	0.27	0.39	0.29	0.41
1968	0.27	0.49	0.27	0.47
1969	0.17	0.44	0.19	0.45
1970	0.25	0.53	0.27	0.54
1971	0.22	0.40	0.25	0.42
1972	0.24	0.30	0.27	0.36
1973	0.31	1.03	0.34	0.84

[a] $\bar{B}$ was determined by taking the mean of the biomasses at the beginning of the year and at the beginning of the next year for the same year-classes.

beginning of the year and the beginning of the following year in each year-class). The annual production (Table 8) ranged from 1.01 to 9.31 kg/ha for fish age 0 through age VI or considering only age I+ from 0.91 to 6.98 or age III+ from 0.42 to 3.07 kg/ha.

Annual production is obviously dependent upon the biomass available at the beginning of the season (B_0), and the effects of other factors upon production will be masked by the differences in available biomass. Annual comparisons may be more evident with the P/B_0 ratio, the production per unit of biomass at the beginning of the year (Table 9). The production per biomass was low from 1956 to 1962, the low water years. The production per biomass also decreased with age:

Age-group	I	II	III	IV	V	V+
P/B_o	2.24	1.00	0.43	0.24	0.16	0.11

Age-groups I and II accounted for 59% of the annual production; 78% by I–III; and 87% by I–IV. The usual P/B ratios using mean biomass are aquivalent to instantaneous growth rates of all year-classes (since $P = \bar{B}G$).

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Dynamics of the Walleye (*Stizostedion vitreum vitreum*) Population in Escanaba Lake, Wisconsin, 1955–72[1]

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KEMPINGER, J. J., AND R. F. CARLINE. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–72. J. Fish. Res. Board Can. 34: 1800–1811.

Harvest and population dynamics of warmwater fish populations in Escanaba Lake have been under study since 1946, when complete creel census was initiated. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) were among the most important species in the sport catch. The purpose of this report is to describe dynamics of the walleye population from 1955 to 1972.

Annual densities of age 3 and older walleye in spring ranged from 13 to 52/ha (mean = 34) and standing crops averaged 12.3 kg/ha. Annual densities of fall fingerlings appeared to be the most important factor influencing size of adult populations. We were unable to isolate factors that governed densities of fall fingerlings. Year-class strength was not affected by water temperatures during incubation nor by size of fall fingerlings. Growth rates of fingerling walleye were density-independent. Survival of fingerlings to age 3 averaged 12% annually; survival was not influenced by size of fingerlings nor by density of potential predators. We found no evidence to suggest that cannibalism had any effect on density of fingerlings or their survival to age 3. Total mortality of adult walleye averaged 47% annually and exploitation rate was 28%. Ricker's (1975) equilibrium yield model was used to assess possible effects of a size limit on walleye yields. We concluded that a size limit would lead to an increase in population biomass, a decrease in growth, and that yields would not change greatly.

Key words: Percidae, population dynamics, *Stizostedion*, harvest, abundance, density, regulations, survival, production, equilibrium yield, biomass

KEMPINGER, J. J., AND R. F. CARLINE. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–72. J. Fish. Res. Board Can. 34: 1800–1811.

On étudie depuis 1946 la récolte et la dynamique des populations de poissons d'eau douce dans le lac Escanaba, alors qu'on entreprenait un recensement au panier complet. Le doré jaune (*Stizostedion vitreum vitreum*) et la perchaude (*Perca flavescens*) figurent parmi les plus importantes espèces dans les prises des pêcheurs sportifs. Le but de ce rapport est de cécrire la dynamique des populations de dorés jaunes de 1955 à 1972.

La densité annuelle des dorés jaunes d'âge 3 et plus au printemps varie de 13 à 52/ha (moyenne = 34), et la biomasse est en moyenne de 12.3 kg/ha. La densité annuelle des fingerlings d'automne semble être le plus important facteur affectant la taille des populations adultes. Nous n'avons pu isoler les facteurs contrôlant la densité des fingerlings d'automne. L'abondance des classes d'âge n'est pas affectée par la température de l'eau durant l'incubation, non plus que par la taille des fingerlings d'automne. Le rythme de croissance des fingerlings de doré jaune est indépendant de la densité. La survie des fingerlings jusqu'à l'âge 3 est en moyenne de 12% annuellement; la survie n'est pas affectée par la taille des fingerlings, ni par la densité des prédatrurs possibles. Nous n'avons aucune preuve que le cannibalisme affecte la densité des fingerlings ou leur survie jusqu'à l'âge 3. La mortalité totale des dorés jaunes adultes est en moyenne de 47% annuellement, et le taux d'exploitation est de 28%. Nous avons utilisé le modèle de rendement d'équilibre de Ricker (1975) pour évaluer les effets possibles d'une limite de taille

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sur les rendements en dorés jaunes. Nous concluons qu'une limite de taille entraînerait une augmentation dans la biomasse de la population, un ralentissement de la croissance et assez peu de changement dans les rendements.

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STUDIES on Escanaba Lake, in northern Wisconsin, have been underway since 1946, to determine effects of liberalized fishing regulations on warmwater fish populations. Regulations included no bag limit or closed season and no size limit, excepting a 56 cm length limit on northern pike (*Esox lucius*), 1964–72. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) were among the most important species in the sport catch. In general, liberalized fishing regulations have had no detrimental effects upon fish populations (Threinen 1951; Patterson 1953; Churchill 1957; Kempinger and Churchill 1972; Kempinger et al. 1975).

Introductions of walleye and northern pike into the lake eventually led to the establishment of both species and appeared responsible for major changes in structure of the sportfish community (Kempinger et al. 1975). Yellow perch was formerly the most numerous species and major predators were smallmouth (*Micropterus dolomieui*) and largemouth bass (*Micropterus salmoides*). Presently centrarchids and yellow perch are at an all time low; smallmouth bass and bluegill (*Lepomis macrochirus*) are approaching extirpation. The community is now dominated by walleye and northern pike with few prey adults.

The purpose of this paper is to describe dynamics of the walleye population during a period of changing community structure, 1955–72. Previously cited studies have reported on development of the walleye population and some of its vital statistics. Here, we briefly summarize these studies and emphasize heretofore unpublished data, with particular reference to growth rates, year-class strength, survival to adulthood, production, and equilibrium yield.

Description of Study Area

Escanaba Lake (lat. 46°04′, long. 89°35′) is located on undeveloped, state-owned land in Vilas County. The watershed is heavily forested and hardwoods predominate. The lake (Fig. 1) has a surface area of 119 ha, a shoreline of 8.2 km, a maximum depth of 8 m, and a mean depth of 4.3 m. As the inlets and an outlet are intermittent, fish migration is probably inconsequential. The shoreline is irregular and there are several small islands with rocky bars. Aquatic macrophytes occur mostly in protected bays.

The lake does not permanently stratify during summer, and temperature differences between the surface and deepest portion of the basin are usually less than 8 deg. C. Concentrations of dissolved oxygen are usually above 5 ppm at all depths, although they may fall below 1 ppm at depths greater than 6 m during temporary stratification. Ice cover generally extends from late November to late April. Over the past 29 yr no winterkills have been observed. Typical concentrations (ppm) of dissolved materials during spring turnover are: nitrate nitrogen 0.3, Kjeldahl nitrogen 0.6, dissolved phosphate 0.08, total phosphate 0.3, and total alkalinity 16. Specific conductance averages 46 μmhos/cm. Concentration of total dissolved solids from a single determination was 25 mg/ℓ.

There are at least 24 species of fish in the lake (Kempinger et al. 1975). Important species in the sport catch have included: walleye, northern pike, muskellunge (*Esox masquinongy*), yellow perch, smallmouth and largemouth bass, rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), and black crappie (*Pomoxis nigromaculatus*). All but the walleye and northern pike are thought to be native to the lake. Between 1933 and 1945 the lake was stocked at irregular intervals with walleye, largemouth bass, yellow perch, northern pike, muskellunge, white suckers (*Catostomus commersoni*), and shiners. Since 1946 the lake was stocked three times with

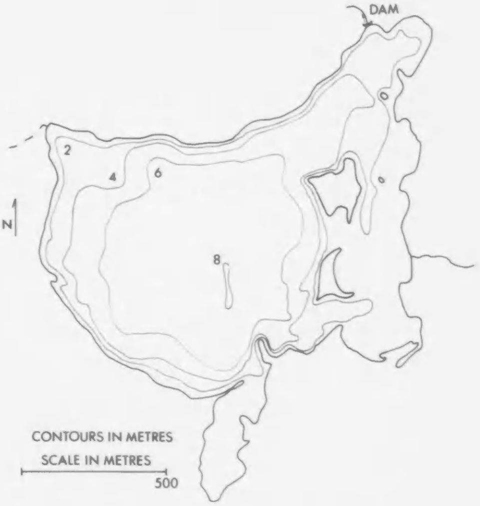

FIG. 1. Hydrography of Escanaba Lake.

muskellunge and four times with walleye; all of these fish were marked by fin removal.

Methods

All anglers were required by law to obtain a permit without charge from the checking station located at the only landing on the lake. Upon completion of each fishing trip, census clerks inspected the catch and recorded numbers of all species. All gamefish and most panfish were measured and weighed, and scale samples collected for age determination. All annual fishery and population statistics were based on a year beginning and ending with ice-out in spring.

Population estimates were made for periods of 8–18 yr for the following species above the total lengths in centimetres indicated: walleye (28), northern pike (30), muskellunge (46), yellow perch (15), pumpkinseed (11), rock bass (10), bluegill (10), and black crappie (15). For convenience we refer to fish of the above sizes as adults. Fish were collected with fyke nets or electroshockers during the spawning season and marked by tagging or finclipping. Population densities were calculated from the Petersen formula using the proportions of marked fish in the anglers' catches. Fall fingerling walleye and in some years age 1 and 2 walleye were estimated by multiple mark and recapture methods using electrofishing gear. We used average survival rates to back calculate numbers of age 1 and 2 walleye from 1955 to 1972 and to calculate expected numbers of adults in 1970 and 1971, when the walleye population was not estimated. Exploitation rates were calculated from the proportions of marked fish in the sport catch.

In some years dart and jaw tags were used, although fin removal was the most common marking technique. Jaw tags probably retarded growth rates, but we do not believe the long-term average growth rates were seriously affected by tagging because usually less than 20% of the adults bore jaw tags.

We examined variations in densities of fingerling walleye in relation to rates of warming and heat buildup of lake water during the spawning and incubation period. Water temperatures are recorded twice daily at the boat landing, which is located in a protected bay. For 3 yr a Taylor recording thermometer was used to monitor water temperatures at one of the major spawning reefs. The probe was placed on the bottom in 60 cm of water. We assumed that water temperatures at the landing were indicative of reef temperatures because there was a linear relationship between daily water temperatures at the landing and on the spawning reef, and slope of the regression line was nearly unity. Temperatures at the landing averaged 2.8 deg. C higher than on the reef. Daily warming rates were estimated from the slope of the regression of average daily temperature and time for 30 days following ice-out.

Production was estimated as the product of instantaneous growth rate and mean biomass. Mean weights were determined from walleye taken by anglers during May. All fish age 6 and older were treated as a single cohort. We used Ricker's (1975) equilibrium yield model to assess the possible effect of length limits on walleye yield. In most simulations we used the long-term average rates of growth and total mortality. Each year was divided into two intervals, May to September and September to the following May. During the former interval 88% of annual growth and 63% of harvest occurred. Because catch rates of legal size fish and mean weight of the catch are important considerations in sport fisheries, these were calculated in addition to yield. Mean weights of individual fish at the midpoint of each interval were calculated assuming constant instantaneous growth rates. Catch in numbers was estimated from the quotient of yield and mean weight at interval midpoint.

Changes in Community Structure

Structure of the sportfish community underwent a major change in the late 1940s. Yellow perch was the most numerous sport species in 1946 and smallmouth bass the major predator (Table 1). Walleye constituted a minor part of community; the first recorded natural reproduction occurred in 1943, though these fish contributed little to the total harvest. Spawning adults were from fry stockings in the 1930s and early 1940s. Large year-classes of walleye produced in 1947 and in subsequent years led to the establishment of the species. Northern pike fry had also been stocked prior to 1946, but it was not until 1957 that a large year-class was produced. Subsequent successful reproduction by northern pike insured maintenance of a large population. Establishment of these two predators appeared to have a marked influence on changes in community structure. In describing these changes we used catch per unit effort (CPE) data from the sport fishery to illustrate population sizes. For most species, population density and CPE were well correlated. Estimates of population densities for walleye and northern pike were available for most years.

Population declines of yellow perch and rock bass were associated with increasing densities of walleye in the late 1940s and northern pike in the early 1960s. Numbers of adult perch declined from about 90,000 in 1946–47 to perhaps less than 1000 in the early 1950s (Fig. 2), when walleye numbers were increasing (Fig. 3). Perch increased in the late 1950s and remained at high levels until 1964. Changes in rock bass densities were similar to those of yellow perch. Smallmouth bass densities also decreased sharply in the late 1940s. Catch of smallmouth bass increased only in 1954 when a single year-class recruited to the fishery. Thereafter, densities declined to low levels and at present they are approaching extirpation. Bluegill, pumpkinseed, and black crappie were minor constituents of the community in 1946, but all these species increased, particularly pumpkinseed, in the late 1950s. Thus, development of the walleye population was associated with an initial decline in smallmouth bass and prey species, followed by an increase in prey adults.

The first large year of northern pike was produced

TABLE 1. Fishing pressure, numbers of fish harvested, and total yields from Escanaba Lake, 1946–75.

Year	Fishing pressure (hours)	Numbers harvested										Yield (kg/ha)
		Smallmouth bass	Largemouth bass	Walleye	Muskellunge	Northern pike	Yellow perch	Pumpkin-seed	Rock bass	Blue-gill	Black crappie	
1946	9,386	635	167	4	14	3	8,803	81	240	26	9	12.9
1947	6,295	421	52	47	7	—	6,121	46	306	31	27	10.1
1948	12,776	385	53	4,313	5	1	9,026	18	224	7	16	22.1
1949	19,332	540	62	2,199	11	2	7,028	95	235	40	12	19.3
1950	35,862	191	49	5,887	34	1	1,210	121	380	33	18	29.9
1951	21,874	57	21	2,267	21	2	843	159	343	95	13	13.2
1952	25,702	156	90	3,791	52	—	393	302	366	71	5	19.4
1953	28,862	636	47	4,683	20	—	728	273	1,563	224	10	19.5
1954	17,965	447	68	2,292	14	1	2,072	376	986	144	8	12.0
1955	23,403	329	146	5,227	9	1	9,006	8,109	1,191	548	63	30.7
1956	24,412	125	161	5,096	6	—	10,251	10,199	1,844	575	645	32.6
1957	24,775	90	283	3,624	13	72	14,612	12,131	1,914	885	1,172	37.4
1958	26,368	54	203	1,178	16	935	15,738	21,740	668	927	1,782	46.1
1959	21,979	130	101	1,010	11	882	7,293	25,792	597	587	1,300	41.6
1960	22,214	86	103	2,469	18	152	12,225	19,164	700	1,876	1,220	40.0
1961	18,497	66	72	3,593	24	294	7,699	10,958	493	1,244	265	27.0
1962	22,367	27	176	2,490	74	691	11,935	9,189	736	730	343	33.2
1963	20,796	10	172	1,352	57	638	8,182	11,170	211	430	394	25.2
1964	12,769	7	137	1,758	22	64	3,926	5,839	76	300	33	14.8
1965	10,775	3	81	1,532	23	73	981	2,463	68	203	108	9.7
1966	13,716	—	25	2,789	22	70	286	38	3	1	24	10.7
1967	14,437	—	1	3,362	21	31	126	1	5	—	4	10.9
1968	9,898	1	1	1,028	24	81	170	32	5	9	3	4.9
1969	11,150	1	—	1,044	32	239	308	42	17	6	8	6.8
1970	14,695	1	2	2,185	33	150	695	34	31	9	5	10.1
1971	16,246	1	2	2,537	25	63	259	16	13	3	—	9.4
1972	11,271	1	2	803	39	103	1,194	26	56	—	—	6.1
1973	13,445	—	1	1,238	25	325	728	2	68	1	5	9.7
1974	11,107	—	—	1,091	13	622	251	2	33	—	80	10.5
1975	17,882	—	9	4,526	25	212	311	4	51	—	33	15.2

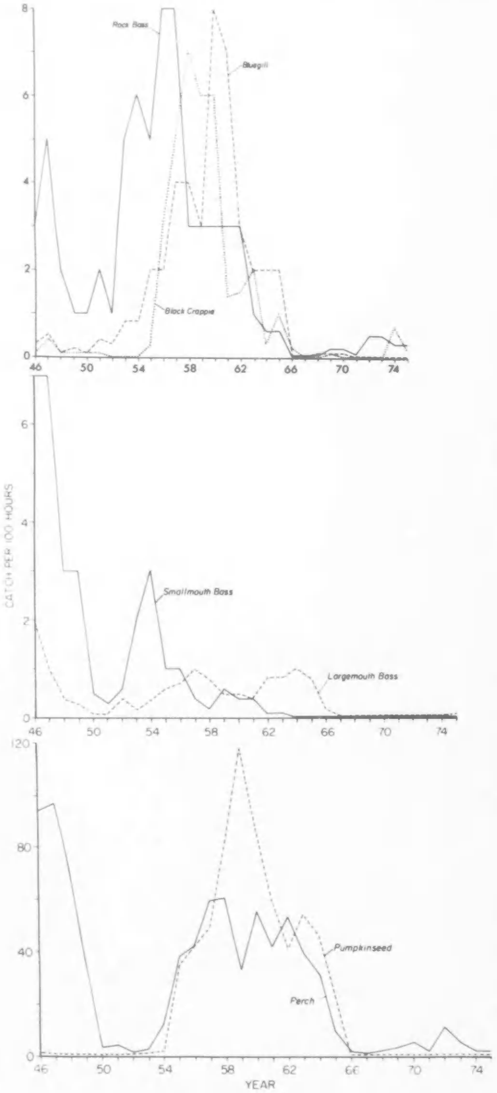

FIG. 2. Annual catches per unit of effort by the sport fishery of centrarchids and yellow perch.

in 1957, when numbers of prey adults were near peak levels. As northern pike densities increased in late 1950s and early 1960s (Fig. 3), numbers of prey adults began a precipitous decline to present low levels. However, decline of prey species did not appear related to a simple increase in predator numbers, because walleye constituted the major portion of the predator component (Fig. 3). Variations in total numbers of predators were due mainly to fluctuations in year-class strength of walleye.

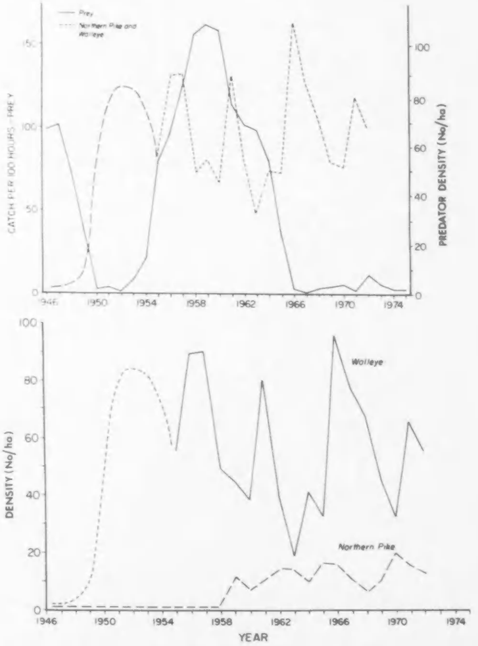

FIG. 3. Annual population estimates of age 2 and older walleye and northern pike (lower panel). Walleye densities for 1946–54 were estimated from sport catches. Number of northern pike captured during 1946–58 were insufficient to calculate population size. Annual catches per unit of effort for all prey species and combined densities of walleye and northern pike are given in upper panel.

We hypothesize that low survival of prey species to adulthood was due to the addition of a littoral predator, the northern pike, to an already dense population of offshore predators, the walleye. Between 1949 and 1956 each of the five prey species produced at least two year-classes large enough to have an effect on the fishery (Table 2). After the first strong year-class of northern pike in 1957, only yellow perch produced relatively large year-classes, in 1957 and 1959. We suggest that the small increase in predators was not nearly as important as the type of predator that was added to the community.

Walleye Population Dynamics

Growth rates — From 1955 to 1969 when structure of the sport fish community underwent marked changes, there were no evident trends in growth rates of adult walleye. At age 4, when both sexes were fully vulnerable to capture by netting in spring, females were about 5 cm longer than males (Table 3). We compared these growth rates with walleye growth data from 15 other

TABLE 2. Year-classes that were large enough to have a measurable effect on the fishery.

Year	Walleye	Northern pike	Smallmouth bass	Largemouth bass	Yellow perch	Pumpkin-seed	Black crappie	Blue-gill	Rock bass
1942				?					*
1943	*		*	?	*				
1944				?	*				
1945									
1946									
1947	*							*	
1948									
1949	*								*
1950	*		*						
1951				*	*			*	
1952					*	*			*
1953						?	*	*	*
1954	*[a]					*	*		
1955	*					?			
1956						*		*	
1957		*			*				
1958	*			*					
1959	*				*				
1960		*							
1961									
1962	*	*							
1963	*								
1964	*	*							
1965	*								
1966	*								
1967	*	*							
1968	*	?							
1969	*	*							
1970	*								
1971									
1972									
1973	*								
1974	*								

[a] 48,000 fingerling stocked in fall.

TABLE 3. Mean lengths (cm) and weights (g) of walleye captured during the spawning seasons, 1965–69, 1972, and 1974. Mean weights were calculated from the linear regression $\log_e W = -5.14 + 3.10 \log_e L$, where W is in grams and L in cm.

	Age							
	2	3	4	5	6	7	8	9
					Length			
Males			35.0	39.5	42.7	45.3	48.7	51.4
Females			39.9	43.1	46.9	51.4	56.1	57.8
All fish	25.9	31.3	35.8	40.9	45.2	49.5	54.1	57.7
					Weight			
All fish	141	254	386	581	794	1,053	1,385	1,684

lakes in the northern part of the state (unpub. data of Snow and Beard, Spooner, Wis.) and growth rates in Escanaba Lake were nearly identical to the average of all lakes.

Most of the variation in annual growth rates of adults could not be accounted for by changes in population density or biomass. We ran a series of linear regressions relating annual, age-specific length increments of males and females to population density and biomass (Fig. 4). Correlation coefficients were consistently negative, but usually were not significant ($P > 0.05$). Some factor or other factors presumably had more influence on growth rates than did population density.

Year-class strength — From 1958 to 1972, estimated densities of fingerling walleye in the fall varied greatly. In 1960, too few fingerlings were captured to permit estimation, and the 1964 year-class was estimated at 265/ha; the 15-yr average was 100/ha (Table 4).

There was no relationship between daily warming rates of the lake and density of fall fingerling walleye ($P > 0.05$). Rates of warming were lowest in 1973 (0.07°C/day) and the 1973 cohort was among the largest. In 1972 and 1975 warming rates were highest, 0.5–0.6°C/day, yet densities of fall fingerlings were well below average. Busch et al. (1975) suggested that the regularity of warming of the lake had an effect on larval survival. They found a positive relationship between daily warming rates (34–45 days after ice-out) and abundance of walleye fry. Fry densities were lowest at warming rates of 0.1°C/day and highest at rates of 0.30–0.35°C/day. We used the correlation coefficients of daily temperature and time as an index of regularity of warming. Addition of this index as an independent variable to daily warming rates did not account for variations in year-class strength.

Busch et al. (1975) reasoned that a short incubation period reduced the time that eggs and larvae would be vulnerable to unfavorable conditions on the reefs. We examined the cumulative degree-days for 30 days after the ice-out, because heat buildup might be more closely associated with incubation time than would rate of warming. Both strong and weak year-classes were produced when lake water remained relatively cool and the relation between cumulative degree-days and density of fall fingerlings was not significant ($P > 0.05$). Warmest incubation periods, in 1972 and 1975, were associated with weak year-classes. For both years we compared temperatures 4 days after ice-out (peak spawning?) and 20 days later (mid-hatch?) with laboratory findings of Koenst and Smith (1976), who examined effects of temperature on fertilization and hatching success of walleye. On the basis of their findings, temperature-induced mortality would not be expected. We conclude that thermal conditions during incubation and hatching had little effect on strength of year-classes, but rather that year-class strength was set at some later time. Forney (1976) reported that mortality of walleye fry and fingerlings in Oneida Lake was much more important in determining year-class strength than was mortality during the first few weeks of life.

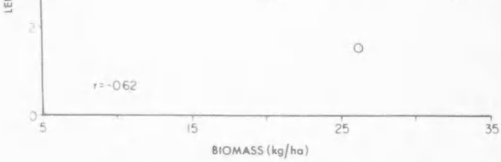

FIG. 4. Biomass of ages 2–9 walleye in spring and annual length increments of age 4 female walleye.

There was no relationships between density of walleye fingerlings in fall and their mean length ($r = 0.10$). When densities of age 1 walleye were added as an independent variable, the correlation was unchanged. By late September length of fingerling walleye ranged from a mean of 94 to 157 mm (15 year Grand mean = 130). Morsell (1970) found that growth of walleye fingerlings in the lake depended upon size of perch fry, their major prey. Walleye growth was highest when they were more than twice as long as perch fry. Growth of walleye fingerlings was lowest when juvenile perch were scarce. Thus, food density and size influenced growth rates of fingerlings, but growth rates were not related to year-class strength.

Population density and survival — Relative densities of age 3 and older walleye depended upon presence of strong year-classes. The adult population was smallest in 1964, when age 3 and 4 fish were from the two weakest year-classes recorded (Table 4). Conversely, the largest adult population, in 1967, was due to the presence of the 1964 year-class, the largest recorded. From 1955 to 1972 density of age 3 and older walleye ranged from 13 to 52/ha (mean = 34) and biomass ranged from 4.2 to 20.7 kg/ha (mean = 12.3). During this period, fingerling walleye were stocked in 1954, 1958, 1959, and 1961 (Table 4), but only the 1954 stock had any effect on population density; 6.5% survived to age 3.

Density of age 3 walleye was related to their density as fall fingerlings. Survival to age 3 of native fingerlings ranged from 3 to 18% (mean = 12; $n = 9$) and survival for 7 of the 9 year-classes ranged from 9 to 14%. Data on when mortality occurs from fingerling to age 3 are

TABLE 4. Estimated densities of walleye in Escanaba Lake, 1955–72. Last values in each row include all older age-groups.

	Age									Total of age 3 and older	
Year	0	1	2	3	4	5	6	7	8+	No.	kg/ha
1955		6,390[b]	1,690[a]							4,900	12.0
1956			1,880[a] 5,390[b]	900						3,250	7.0
1957			5,130	1,000 3,150[b]						5,530	13.7
1958	4,500 35,800[b]	770[a]	120[a]	2,700	320 1,900[b]	130	130	515		5,695	20.7
1959	25,700 11,000[b]	1,900	370[a]	60	2,560	320 1,450[b]	120	420		4,930	18.7
1960	[c]	12,600	1,160	200	45	1,490	200 1,020[b]	280		3,235	10.9
1961	750 21,000[b]		6,000[a]	610	100	60	1,050	290 1,300[b]		3,410	7.5
1962	14,400	340[a]		3,190	380	35	85	500	510[b]	4,700	16.4
1963	13,200	6,540[a]	260[a] 310[b]		870	20		420	350[b]	1,660	6.0
1964	31,400	6,000[a]	3,330[a]	140 160[b]		410	60	335	390[b]	1,495	4.2
1965	10,600	14,250[a]	1,170	1,760	60 90[a]		520		275[b]	2,705	7.6
1966	22,200	4,810[a]	8,180[a]	1,320	990	500			225[b]	3,035	9.6
1967	8,700	10,100[a]	2,800[a]	4,360	785	430	580			6,155	18.4
1968	8,500	3,950[a]	3,720[a]	1,500	1,760	250	370	200		4,080	14.5
1969	19,300	3,860[a]	1,045[a]	1,980	760	1,050	190	75	125	4,180	13.7
1970	10,100	8,760[a]	1,020[a]	560[a]	1,055[a]	400[a]	560[a]	100[a]	110[a]	2,785	
1971	3,100	4,580[a]	1,090[a]	3,900[a]	1,940[a]	270[a]	220[a]	250[a]		6,580	
1972	1,600	1,400[a]	2,280[a]	580	2,090	1,040	140	120	230	4,200	15.1

[a] Calculated from mean survival rates.

[b] Stocked as fingerlings.

[c] Too few captured to estimate density.

limited. Overwinter survival rates of fall fingerlings from the 1958 and 1959 year-classes were 42 and 49%, respectively. Survival of the 1964 year-class from fall fingerlings to fall yearlings was 32%. Annual survival of the 1958 year-class from age 1 to 2 and age 2 to 3 were 61 and 52%, respectively. If these estimates are indicative of other years, mortality appears to be relatively high until after completion of the second growing season.

Despite the wide range in mean length of fall fingerlings, length of fingerlings and survival to age 3 were not related. Some age 1 and 2 walleye are taken by sportfishing. Though exploitation of age 2 fish was directly related to fishing pressure (Kempinger et al. 1975), harvest of age 1 and 2 walleye had little effect on survival from fingerlings to age 3.

Annual survival rates of age 3 and older walleye from 1960 to 1969 ranged from 31 to 68% (mean = 53). We did not use survival rates for 1958 and 1959 in computing mean survival rates; according to successive point estimates only 400 walleyes died between April 1958 and April 1959, yet over 1100 were recorded in the sport catch during the year. Exploitation rates ranged from 13 to 42%, but in most years exploitation had little effect on total mortality (Fig. 5). It was only during 1962 and 1967 when exploitation rates were 37 and 42%, that total mortality rates noticeably increased.

Although fishing mortality was important in some years, the density of fall fingerlings and their survival to age 3 appeared to be the most important factors controlling adult densities. We examined density of fall fingerlings and survival to age 3 in relation to density of adult walleye to explore possible importance of cannibalism. None of the correlations between density of fingerlings, their survival to age 3, and densities of adult walleye approached significance. Addition of northern pike densities as an independent variable failed to improve correlations.

Theumler (1969) did not find a single juvenile

TABLE 5. Annual instantaneous growth rates (G), mean biomass ($\bar{B}$), and production (P) of Age 2 and older walleye from May 1966 to May 1969.

	1966			1967			1968		
Age	G	$\bar{B}$	P	G	$\bar{B}$	P	G	$\bar{B}$	P
2	0.580	399	232	0.464	401	186	0.492	473	233
3	0.282	975	275	0.351	889	312	0.655	364	238
4	0.221	281	62	0.238	213	51	0.532	657	348
5	0.185	282	52	0.060	226	14	0.511	140	71
6[a]	0.060	550	33	0.059	467	28	0.039	395	16
Total		2,487	654		2,196	591		2,029	906
Total (kg/ha)		20.8	5.5		18.3	4.9		16.9	7.6
P/$\bar{B}$		0.263			0.269			0.446	
Yield (kg/ha)		8.7			10.0			3.7	

[a] Includes all older age-groups.

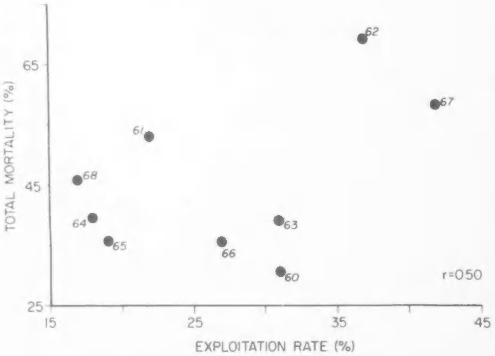

FIG. 5. Annual rates of exploitation and total mortality of adult walleye. Numerals indicate fishing years.

walleye in stomachs of adults, even in 1967, when density of juvenile perch was low and incidence of invertebrates in walleye stomachs was high; he examined 688 stomachs of age 1 and older walleye collected in 1967 and 1968. We also examined growth rates and condition factors of adult walleye in relation to density of fall fingerlings. Both strong and weak year-classes were produced in years when adults grew slowly. Although cannibalism may have had an effect on year-class strength, we found no evidence to support this hypothesis.

Production — We calculated annual production from May 1966 to May 1969, years in which there were no stocked walleye in the population. Annual production ranged from 4.9 to 7.6 kg/ha and was most influenced by instantaneous growth rates (Table 5). The P:$\bar{B}$ ratio, which is the mean weighted growth rate of the population, was about 70% greater in 1968 than in 1966 and 1967. Even though biomass was lowest in 1968, production was high because of high growth rates.

Annual yield of walleye from 1966 to 1968 was not directly related to annual production (Table 5). Although production was highest in 1968, yield was low because exploitation rates were well below average, 17 vs. 29%. When populations are in equilibrium and natural mortality is low, yield should approximate annual production, but this may only be evident when long term averages are compared.

Yields — Under liberalized fishing regulations, walleye yields from 1948 to 1975 ranged from 3 to 26 kg/ha (mean = 9). During this period fishing pressure ranged from 83 to 302 h/ha (mean = 158). Fishing pressure and yield were poorly correlated, because pressure was influenced by availability of panfish and exploitation rates of walleye varied greatly, from 13 to 42% (Kempinger et al. 1975). Although annual exploitation rates of walleye fluctuated considerably, a substantial number of fish present as age 3 were ultimately harvested. For example, between 1951 and 1963 cumulative harvest of individual cohorts from age 3 to 7 ranged from 50 to 89% (mean = 69).

In Escanaba Lake, as in other lakes, annual exploitation rates were apparently influenced by forage density and growth rates of walleye (Forney 1967; Schupp 1972; Kempinger et al. 1975). When growth rates were relatively low, exploitation rates were high. Hence, the effect of fishing on total mortality was mediated by food supply. Though fishing under liberalized regulations has had no detrimental effect on the walleye population in Escanaba Lake, it is conceivable that walleye populations might be overexploited under high sustained fishing pressure and several consecutive years of low forage.

Equilibrium yield — When average rates of growth and mortality were used in Ricker's

TABLE 6. Equilibrium yield calculations for walleye with 100 kg of annual recruits. Total annual mortality was 47%, average exploitation rate was 28%, and instantaneous growth rates were calculated from data in Table 3. Three simulations were: (1) Instantaneous growth rates (G) and natural mortality (M) unchanged, (2) G was decreased by 10%, and (3) M was increased to 1.1M when fishing mortality (F) was set to 0.

Age of recruits to fishery	Approx. size limit (cm)	Yield (kg)	Catch (No.)	Mean wt. of catch (kg)	Population biomass (kg)
G and M unchanged					
2	—	151	360	0.42	442
2+	30	156	312	0.50	502
3	31	157	291	0.54	536
3+	35	163	251	0.65	638
4	36	165	226	0.73	698
4+	40	167	194	0.86	804
5	41	165	176	0.94	864
5+	45	161	149	1.08	967
G decreased by 10%					
2	—	134	353	0.38	394
2+	30	137	311	0.44	448
3	31	138	294	0.47	478
3+	34	140	250	0.56	566
4	35	140	226	0.62	618
4+	39	139	193	0.72	706
5	39	137	176	0.78	757
5+	42	132	148	0.89	842
M → 1.1M when F → 0					
2+	30	154	308	0.50	496
3	31	151	280	0.54	518
3+	35	156	240	0.65	612
4	36	155	212	0.73	662
4+	40	155	180	0.86	757
5	41	150	160	0.94	806
5+	45	145	134	1.08	897

(1975) equilibrium yield model, predicted peak yield occurred when walleye were first harvested as age 4 in fall (Table 6). Peak yield was only 10% greater than yield with no size limit. With a 40 cm size limit, catch would be reduced by 46% and mean weight of the catch would be more than twice that under no length limit. Because a size limit would have the greatest effect on catch and mean weight of catch, implementation of such regulations would depend upon fishermen attitudes rather than biological considerations.

An important effect of length limits would be an increase in population biomass. At peak yield, biomass would be 82% greater than predicted with no size limit. In the above example it was assumed that growth and natural mortality rates did not change with increasing levels of protection. We suspect that, if walleye biomass were to increase by 50% or more above the long term average, growth rates would decline. When we decreased instantaneous growth rates of all age groups by 10%, predicted yields at all levels of protection were below yield with no length limit (Table 6). With a size limit of 40 cm, yield was 15% less than that predicted with no change in growth rates.

One possible consequence of a size limit would be a compensatory increase in natural mortality of protected age-groups. This would be analagous to hooking mortality of sublegal fish. When we increased natural mortality by 10%, i.e., M → 1.1M, when an age-group was protected, predicted yields at all size limits were similar to yields with no protection (Table 6).

We conclude from this analysis that length limits would not result in increased yields of walleye in Escanaba Lake. Though the equilibrium yield model may be applied without knowledge of actual population density, it seems that such information is essential in judging the likelihood of compensatory changes in growth. Even small changes in growth led to sizeable decline in predicted yield. We have no measure of compensatory changes in natural mortality or of hooking mortality of sublegal fish. However, small increases in mortality also resulted in decreased yields. We suggest that the equilibrium yield model would be most useful in choosing length limits where populations are fast growing, highly exploited, or both. We question the applicability of the model to many walleye populations in northern Wisconsin, because exceptionally fast growing populations are uncommon and exploitation rates are typically less than 30%.

Discussion

Since 1955 densities of adult walleye have varied by fourfold and were most influenced by annual variations in year-class strength. Neither rates of lake warming in early spring nor size of fall fingerlings appeared related to fingerling densities or their survival to age 3. The relation between summer water temperatures and growth or survival of fingerlings merits further investigation. Above normal water temperatures during summer have been correlated with strong year-classes for several percids (Svärdson and Molin 1973, Kipling 1976).

We found no evidence to suggest that cannibalism affected year-class strength. Numbers of fingerlings surviving to age 3 appeared independent of adult densities. Cannibalism should be most evident when forage densities are low and growth rates of adults are slow (Forney 1976), but even under these conditions, no juvenile walleye were found in adult stomachs. It is possible that cannibalism was a density-independent process, hence, our methods of analyses would not have detected it. In fact, few relations we examined were density-dependent.

Marked changes in the sportfish community have been linked to the introduction of exotic predators (Kempinger et al. 1975). As walleye became abundant in the lake, smallmouth bass densities declined and never recovered as did other centrarchids and yellow perch. Eschmeyer (1950) reported a similar decline in smallmouth bass after walleye was introduced in Lake Gogebic. Displacement of smallmouth bass by walleye in other northern Wisconsin lakes appears to have been common during the 1940s when walleye were widely stocked. However, we have been unable to obtain documentation of these alleged shifts in predominant species.

As northern pike numbers increased in the late 1950s, densities of all prey adults declined and have remained low. Presently, walleye represent the largest proportion of ichthyomass and northern pike rank second. This community structure has persisted for about 9 yr and has been observed in other lakes of the region. In Big Sand Lake (398 ha), Niemuth and Klingbiel (1960) estimated the biomass of age 1 and older walleye at 20 kg/ha of age 1 and that of perch at 6 kg/ha. Bever and Lealos (1974) found a density of 59/ha of age 1 and older walleye in Pike and Round lakes (607 ha). In this chain of lakes walleye are abundant and slow-growing, and prey species represent a minor portion of total fish biomass. Presumably in lakes such as these, a small number of prey adults are able to produce large numbers of juveniles that sustain the predators. Juvenile prey, therefore, suffer high mortality rates and few survive to adulthood.

Walleye and northern pike responded differently to changes in community structure. Walleye growth rates have not changed over the past 15 yr despite large variations in densities of adult prey. Initially, northern pike grew rapidly when their population was building in the late 1950s (Kempinger and Carline 1977). As their densities increased, growth rates began a steady annual decline from 1959 to 1971. Thus, reduced prey populations have had more effect on northern pike than on walleye. Perhaps, walleye were better able to exploit alternate food resources, than were northern pike.

From results of equilibrium yield calculations we concluded that length limits would not lead to increased walleye yields because of possible compensatory changes in growth and natural mortality. Recent analyses of changes in yield from a length limit on northern pike provides an interesting parallel. Size limit at which peak yield was predicted from equilibrium yield model was close to the 56-cm length limit that was implemented in 1964. During the 8 yr the length limit was in effect, average annual yield of northern pike declined by 73% (Kempinger and Carline 1977). Of the parameters assumed to remain constant in the equilibrium yield model, growth rates declined by about 40%, natural mortality increased from 14 to 76%, and recruitment rates more than doubled. At least for northern pike, it was clear that compensatory changes in growth and mortality had profound effects on numbers of legal size fish available to anglers. From analysis of walleye data it appeared that even changes of small magnitude in growth or mortality had significant effects on predicted yields. Ultimate utility of yield models appears dependent upon one's ability to reasonably predict magnitude of compensatory adjustments in population parameters.

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Evidence of Inter- and IntraSpecific Competition as Factors Regulating Walleye (*Stizostedion vitreum vitreum*) Biomass in Oneida Lake, New York[1]

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FORNEY, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

The sequence of events that led to a decline in numbers of American eel (*Anguilla rostrata*) and esocids and an increase in numbers of walleye (*Stizostedion vitreum vitreum*) in Oneida Lake from 1900–74 are reviewed. Demise of eel and esocids was followed by a rise in numbers of walleye, but little change in mean size of individual walleye. Reduced interspecific competition apparently enhanced walleye recruitment, but the anticipated increase in growth of walleye was probably inhibited by intensified intraspecific competition. This interpretation was supported by evidence that recruitment and growth of walleye in 1957–74 were regulated by prey abundance. Transition from a diverse predator population to one dominated by walleye was orderly and yellow perch (*Perca flavescens*) remained the most abundant prey.

Key words: Percidae, competition, walleye biomass, *Stizostedion*, population dynamics, community ecology

FORNEY, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

L'auteur passe en revue la succession d'événements qui aboutirent à un déclin de l'anguille d'Amérique (*Anguilla rostrata*) et des ésocidés, et à une augmentation de l'abondance du doré jaune (*Stizostedion vitreum vitreum*) dans le lac Oneida entre 1900–1974. La diminution de l'anguille et des ésocidés fut suivie d'une augmentation du doré jaune, sans qu'il y ait eu beaucoup de changement dans la taille moyenne des dorés jaunes individuels. Une compétition interspécifique moins forte a favorisé, semble-t-il, le recrutement des dorés jaunes, mais l'augmentation anticipée du rythme de croissance des dorés jaunes a été probablement retardée par une compétition intraspécifique plus intense. Le fait que le recrutement et la croissance du doré jaune entre 1957–1974 ont tous deux été réglés par l'abondance des proies confirme cette interprétation. La transition d'une population à prédateur divers à une dominée par le doré jaune se fit de façon ordonnée, et la perchaude (*Perca flavescens*) demeura la proie la plus abondante.

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THIS paper examines the response of walleye in Oneida Lake to a reduction in abundance of other piscivorous fish between 1900 and 1975. During this period populations of northern pike (*Esox lucius*) and the American eel (*Anguilla rostrata*) declined and chain pickerel (*Esox niger*), once abundant, approached extinction. In contrast, the walleye (*Stizostedion vitreum vitreum*) prospered and became the predominant predator. A descriptive account of the early fishery and fish populations by Adams and Hankinson (1928) and records of the Oneida Fish Hatchery reveal major trends but finer details of species interactions are obscure. Consequently, interpretation of historical events rests heavily on inferences drawn from studies of the contemporary walleye population (Forney 1967, 1974, 1976). Some of the relations adduced border on speculation but may contribute to an understanding of competition.

Background

Oneida Lake has a maximum depth of 16.8 m, a mean depth of 6.8 m, and a surface area of 20,700 ha. The lake is chemically productive as evidenced by an alkalinity of 80 ppm, total dissolved solids of 163 ppm, and a mean total phosphorus (PO_4) concentration of 0.13. Morphometric and chemical features of the lake are described in detail by Greeson (1971). Oglesby and Schaffner (1976) estimated the

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phosphorus loading at 0.72 g $P \cdot m^{-2} \cdot yr^{-1}$. On the basis of Vollenweider's index of eutrophication (Michalski et al. 1973), the lake borders between meso- and eutrophic. Wind action and currents generally maintain isothermal conditions during the summer, although temporary stratification may develop during extended periods of calm weather. Ice cover usually forms in mid- to late-December and persists through March.

Cultural disturbances — The initial wave of immigrants settled in the lake basin between 1790 and 1810. By 1890 most of the arable land was in agricultural production. Later, much of the cultivated land at higher elevations in the basin was abandoned, but truck farming intensified and extensive wetlands bordering the south shore of the lake were drained between 1915 and 1935.

The lake became an important link in the route from the eastern seaboard to the Great Lakes with the completion of the Barge Canal in 1916 (Barber 1963). Regulation of water levels in the system and construction of dams on the Oswego River and at the outlet of Oneida Lake probably had a profound effect on the fish community. Manipulation of water levels in the spring, designed to reduce property damage, also reduced flooding of marshes, where northern pike and chain pickerel spawned. Stabilization of water levels promoted extensive urbanization of the shoreline (Greeson 1971), which further degraded lowlands near the lake which were potential spawning grounds. Whether dams and locks were an effective barrier to migration of eels from Lake Ontario is unknown, but the eel fishery was abandoned about 20 yr after completion of the Barge Canal.

Greeson (1971) concluded that cultural eutrophication of the lake has proceeded slowly and cited as evidence that only 20% of the phosphorus entering the lake originated from the 87,000 people residing in the basin in 1967. However, the most significant shifts in land use predate quantitative studies of nutrient input, and the effect of nonpoint sources of nutrients on the trophic status of the lake is uncertain.

Biological changes — Dense stands of emergent vegetation occupied much of the shoreline as late as 1927 (Baker 1916, 1918; Adams and Hankinson 1928). In most bays bands of bulrush (*Scirpus* sp.) and water willow (*Dianthera* sp.) extended 100 to 300 m from shore, whereas scattered stands lined the more exposed shoreline. Emergents were sparse in 1946 (Burdick and Lipschuetz unpublished data) and by the 1950s only remnants of the once vast beds remained and these were largely restricted to the littoral area bordering undeveloped islands. Shoreline development and changes in water level regimes may have contributed to the disappearance of emergents but the exact cause is obscure.

In contrast, submersed macrophytes have remained moderately abundant and beds extend to a depth of 3 m in some bays. Baker (1916) observed that macrophytes grew to a depth of 2.4–3.0 m in 1915, suggesting that the depth of light penetration has not decreased. Muenscher (1928) reported an average Secchi disc transparency of 3.5 m in the summer of 1927, within the range of 1.6–3.9 observed in recent years.

Changes in the composition of the benthos are well documented. Ephemeroptera and Trichoptera were common in the littoral area of Lower South Bay in 1917 (Baker 1918) but few representatives of these families were present in 1967 and tubificids exhibited a marked increase (Clady 1975). In deeper areas of the open lake the burrowing mayfly, *Hexagenia limbata*, was the predominant form (Baker 1916) and the density averaged 256 $nymphs \cdot m^{-2}$ in 1956–58 (Jacobsen 1966). The population was sharply reduced in 1959, when oxygen concentration declined to 2 $mg \cdot \ell^{-1}$ over 50% of the basin and to 0.5 $mg \cdot \ell^{-1}$ in some areas. Temporary oxygen deficits recurred in the 1960s and chironomids quickly replaced mayflies. By 1967 *H. limbata* was extinct (Clady and Hutchinson 1976).

Although shifts in species composition of the benthos in Lower South Bay are symptomatic of enrichment, modification of the shoreline and greater shoreline erosion following the disappearance of emergent vegetation may have induced changes in benthos that mimic the effects of enrichment. Eutrophication also seems like an oversimplistic explanation for the abrupt deterioration in oxygen concentrations that let to extinction of the mayfly. Development of anaerobic conditions was not preceded by an identifiable increase in nutrients, nor is there any strong evidence of increased algal density during the past 60 yr judging from the depth distribution of macrophytes. The possibility that conditions that triggered the deoxygenation of deeper basins was a unique climatic event cannot be ruled out, since oxygen depletion was temporary and associated with hot, calm weather. If burrowing by the large *H. limbata* population contributed to aeration of sediments and maintained a delicate balance between sedimentation and oxidation of organic material, a decrease in mayfly density might increase the probability of recurrent oxygen deficits in subsequent years.

Characteristics of the fishery — Early conflicts between commercial and sport fishermen were resolved in favor of sport fishermen. Netting was prohibited after 1900, although sale of walleye and most other species caught by hook and line was permitted until 1960. C. F. Davison, a fish dealer and former commercial fisherman, estimated the total catch in 1928 was 226,000–272,000 kg, or 11–13 $kg \cdot ha^{-1}$ (Adams and Hankinson 1928).

Walleye, chain pickerel, yellow perch, and smallmouth bass (*Micropterus dolomieui*) were considered the most important sport fish in the 1920s by Adams and Hankinson (1928) and with the exception of the chain pickerel have remained important. The numbers harvested in 1957–59 were 9.9 walleye, 9.6 yellow perch, 1.1 smallmouth bass, and 4.8 other $fish \cdot ha^{-1} \cdot yr^{-1}$ (Grosslein 1961). Based on the average weights of these species (unpublished data) the annual yield was 9.6 $kg \cdot ha^{-1} \cdot yr^{-1}$.

Exploitation of walleye was 10, 14, and 47% of estimated spring populations in 1957–59, respectively (Forney 1967). Rates of exploitation in other years were probably equally variable. Although the catch was not monitored, total annual mortality determined from successive population estimates ranged from 0.16 to 0.68 and averaged 0.34 between 1960 and 1974.

Population changes — The eel, walleye, chain pickerel, and northern pike were important piscivorous species in the early 1900s (Adams and Hankinson 1928). Of these only the walleye remained abundant. The magnitude of the early predator populations is unknown but some indication of their relative abundance can be inferred from descriptive accounts of the fishery. Cobb (1905) described the ice fishery in 1902 and estimated that 8000 kg of pickerel and 10,000 kg of walleye were caught on tip-ups. Adams and Hankinson (1928) implied that walleye and pickerel were about equally abundant in the 1920s and indicated that northern pike were not as numerous as pickerel. Van Cleave and Mueller (1934) examined the parasites of Oneida Lake fish in 1930–31 and noted that the numbers of different species examined by them were chiefly a reflection of their relative abundance. Their samples, taken in gill nets, trammel nets, and trap nets, included 58 walleye, 68 chain pickerel, and 19 northern pike. Apparently the esocid populations had collapsed by the winter of 1945–46, when the N.Y.S. Conservation Department conducted a post-card survey of the angling catch. The reported catch included 5032 walleye and only 127 esocids. In recent years northern pike have remained scarce and the pickerel population has approached extinction.

The eel must have ranked as an important predator, since the reported catch of 18,900 kg of migrants in 1913 represented a yield of 0.9 kg·ha^{-1} (Adams and Hankinson 1928). A fairly high stock biomass would be required to maintain this yield, since eels mature at an advanced age. In Lake Ontario eels migrate at age XIII–XV and from age and growth data presented by Hurley (1972) a ratio of yield to stock of 1:5 appears reasonable if premigration mortality is negligible. This suggests a biomass of at least 4.5 kg·ha^{-1} in Oneida Lake in the early 1900s, and possibly a substantially higher biomass if weirs were inefficient or if the actual catch was considerably higher than the reported catch as suggested by Adams and Hankinson. The eel fishery was abandoned in the 1930s and only an occasional specimen has been taken in recent years.

Although the chain pickerel and eel occupied the littoral area their loss had little detectable effect on the structure of the inshore fish populations. Clady (1976) compared catches in 104 seine hauls made in 1915–27 with catches in 520 seine hauls taken in 1960–70. Frequency of capture was used as a measure of abundance, since differences in gear and seining technique negated direct comparison of numbers captured. Yellow perch was the species taken most frequently in shore seining in both periods and it was clearly the predominant species in 1960–70. Among 16 other species that occurred in over 10% of the catches in 1915–17, 10 were captured in about the same proportion of the seine hauls in 1960–70. Two potential prey species, logperch (*Percina caprodes*) and white suckers (*Catostomus commersoni*), showed some increase in frequency of capture, whereas silvery minnows (*Hybognathus nuchalis*) and spottail shiners (*Notropis hudsonius*) were taken less frequently. However, species composition of the population showed relatively little change over the 50-yr period considering temporal and spatial differences in sampling effort. Only one species not present in 1915–27, white perch (*Morone americana*), appeared in more than 10% of the seine hauls in 1960–70.

The white perch probably invaded the lake from the Mohawk–Hudson River system via the Barge Canal in the late 1940s and subsequently spread through central New York (Scott and Christie 1963). A series of successful yearclasses were produced in the early 1950s and the population was well established by 1959 (Alsop and Forney 1962). In later years, the catches of age I and older white perch in gill nets declined, although in some years substantial numbers of young were taken in bottom trawls (Table 1). Predation probably played an important role in limiting expansion of the white perch. Numbers of white perch recruited to the adult stock in 1961–68 were more closely correlated with abundance of age 0 yellow perch than with abundance of age 0 white perch (Forney 1974). Apparently young white perch only survived in appreciable numbers in years when young yellow perch were sufficiently abundant to reduce intensity of predation.

Other invaders failed to proliferate or collapsed after an initial surge. Freshwater drum (*Aplodinotis*

TABLE 1. Trends in abundance of young and older white perch in Oneida Lake, 1959–73.

Year	Age 0[a]	Age 1 and older[b]
1959	9.3	15.1
1960	224.3	31.5
1961	69.6	6.5
1962	28.0	9.5
1963	5.1	13.3
1964	5.1	15.5
1965	86.9	16.9
1966	102.8	8.6
1967	14.8	7.1
1968	1.1	3.1
1969	7.7	4.3
1970	16.4	11.7
1971	10.8	3.0
1972	2.9	1.6
1973	205.9	1.9

[a] Mean catches in trawls August–October. Area swept per haul, 1000 m^2.

[b] Mean catches in 200 yd of gill net with equal lengths of 3.8-, 5.1-, 6.4-, 7.6-, 8.9-, and 10.2-cm stretched mesh.

grunniens) and gizzard shad (*Dorosoma cepedianum*) were first observed in the lake in the early 1950s (Dence and Jackson 1959). A few large drum were caught by anglers and some were taken in experimental nets in later years. Although intensive annual surveys were begun in 1959 to estimate abundance of young-of-the-year fish, young drum were not detected until 1973, when a few were taken in trawls and some appeared in stomachs of walleyes. Presence of gizzard shad had not been reported before 1954, when vast schools of young attracted public attention (Dence 1964). The explosion was brief and perhaps only one or two large year-classes were produced. After 1956 an occasional adult was encountered but there was no further evidence of successful reproduction until 1973, when a few young were taken in seines.

The overwhelming predominance of percids in recent years is illustrated by catches in experimental gill nets set annually at depths of 3–10 m at 15 sites during June–September from 1958 to 1973 (100 ft of 3.8-, 5.1-, 6.4-, 7.6-, 8.9-, and 10.2-cm stretched mesh set overnight). The average numbers per lift were:

Yellow perch (*Perca flavescens*)	94.6
Walleye (*Stizostedion vitreum vitreum*)	32.5
White perch (*Morone americana*)	9.7
White sucker (*Catostomus commersoni*)	3.1
Cisco (*Coregonus artedii*)	2.1
White bass (*Morone chrysops*)	1.4
Pumpkinseed (*Lepomis gibbosus*)	0.9
Smallmouth bass (*Micropterus dolomieui*)	0.8
Channel catfish (*Ictalurus punctatus*)	0.8
Rock bass (*Ambloplites rupestris*)	0.5
Brown bullhead (*Ictalurus nebulosus*)	0.2
Carp (*Cyprinus carpio*)	0.2
Burbot (*Lota lota*)	0.2

Walleye and yellow perch constituted about 85% of the gillnet catches and these two species were nearly as well represented in trawl and trap-net catches during the same period.

Response of Walleye to Reduced Interspecific Competition

The catch of walleye in trap nets fished during the spawning run rose substantially from 1926 through the early 1940s as eel and esocids declined, but the average size of females caught did not change. Apparently, reduced competition with eel and esocids for prey enhanced walleye recruitment but the rise in walleye biomass intensified intraspecific competition for food which stabilized walleye growth. This interpretation was strengthened by evidence that growth and recruitment of walleye in 1954–73 were governed by prey abundance.

Walleye abundance — Trap nets were set by the Oneida Hatchery at the mouth of Scriba Creek, a tributary, and at intervals along the shore to intercept spawning walleye from 1926 to 1974. Daily catch records (not shown) clearly indicated that the 11- to 17-day period the nets were fished consistently bracketed the peak of the spawning run.

The catch of females per net-day (CPE) is shown in Fig. 1. The rise in CPE probably reflected a real change in abundance of the Scriba Creek spawning population, since the gear and fishing methods were not significantly altered and early reports suggest that the demand for eggs usually exceeded the supply. Sensitivity of the trap-net catch as an index of spawning stock in the lake was tested by comparing CPEs during the spawning runs with the estimated numbers of mature females available. The populations of age IV and older walleye were estimated by mark and recapture in 1957–74 (Forney 1967 and unpublished data). These estimates were halved, since the sex ratio was approximately 1:1, and the percentages of females that were mature were approximated from data on age composition and age at maturity collected concurrently (Forney 1965 and unpublished data).

The CPE of females was responsive to fluctuations in adult stock between 1957 and 1974 (Fig. 2). Much of the variation not associated with stock density seemed related to the number of nets set. The disproportional increase in CPE after 1968, when generally fewer nets were set, suggests that the less productive sets were eliminated or there was considerable gear interference. A simple linear regression indicated that differences in adult stock accounted for about half ($r^2 = 0.48$) the variation in CPE from 1957 to 1972. Inclusion of number of nets set as a second independent variable in a linear multiple regression accounted for much of the remaining variation ($R^2 = 0.84$).

A more refined estimate of the adult female stock in 1926–74 was derived from the observed relations between catches, numbers of nets fished, and population densities in 1957–74 (Fig. 3).

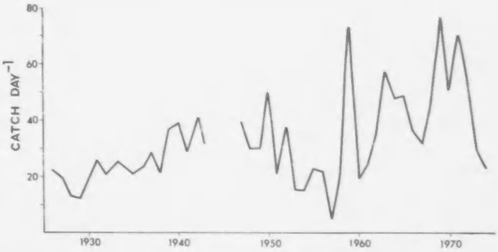

FIG. 1. Mean catches of female walleye per day in trap nets set by the Oneida Hatchery during the spawning period in 1926–74.

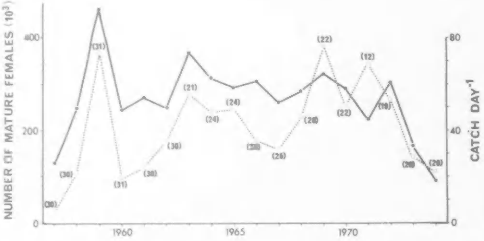

FIG. 2. Population of mature female walleye estimated by mark and recapture in April (solid line) and catches of females per day in nets set by the Oneida Hatchery during the spawning period in 1957–74. Number of trap nets fished in parentheses.

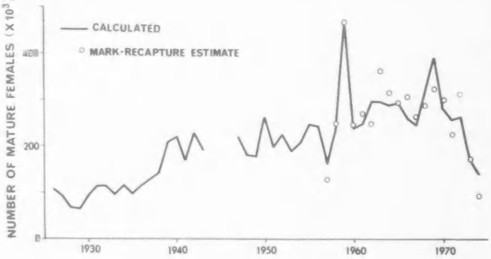

FIG. 3. Number of mature female walleye in 1926–74 based on the catch per day (Fig. 1) and adjusted to conform with the relation between effort and female stock observed in 1957–74 (Fig. 2).

Although the estimates of adult stock suggest a threefold increase in density over the 48-yr period, the exact magnitude must be viewed with some caution, since changes in hatchery operation, netting techniques, and shifts in distribution of spawning fish are possible, if not likely, over an extended period. However, close agreement between stock density predicted from catch–effort data and values estimated by mark and recapture strengthens the conclusion that the number of walleye increased substantially during a period when abundance of other predators was decreasing.

Size composition and growth — The apparent increase in abundance of walleye was not accompanied by a change in average size of adults. Few walleye were measured before 1950, but the average weights of mature females can be inferred from the total litres of eggs collected by the Oneida Hatchery and the numbers of females processed. Litres of eggs per female should be a reliable index of weight since fecundity of walleyes is roughly proportional to weight (Wolfert 1969). Volume of eggs per female fluctuated widely but there was no evidence of a trend over the 50-yr period (Fig. 4). To determine whether volume of eggs per female was a sensitive measure of size composition of the adult stock, litres of eggs per female processed were plotted against mean observed weights of samples of 300–500 females taken in eight spawning runs between 1956 and 1973 (Fig. 5). Most of the variation in volume of eggs per female was attributable to differences in weight of female walleye processed in these years. Apparently the mean weight of females in the Scriba Creek spawning run has averaged about 0.8 kg since 1926 and has varied within a fairly narrow range of 0.6–1.0 kg.

The stable size composition of the adult stock is consistent with data that shows that growth of age IV and older walleye was stable between 1943 and 1973 (Forney 1965 and unpublished data). Individual year-classes displayed only modest variation in mean length as exemplified by a range of 39–43 cm for age V females. Although growth data for year-classes produced before 1939 are not available, the stable size composition of the adult population suggests that

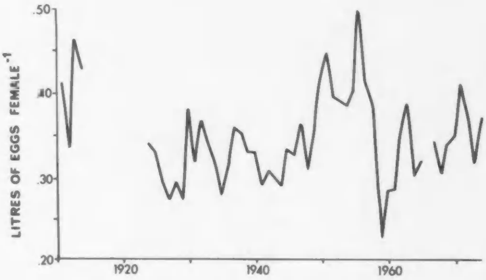

FIG. 4. Volumes of eggs per female from walleye processed annually by the Oneida Hatchery, 1911–74.

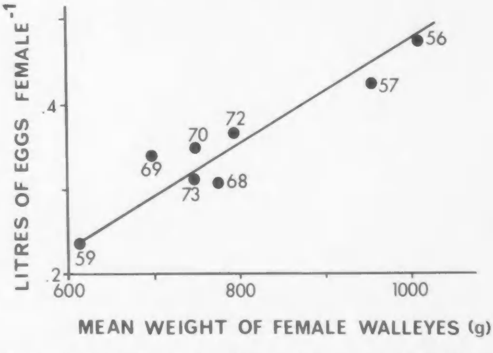

FIG. 5. Relation of volume of eggs per female to mean weight of females processed by the Oneida Hatchery in 8 yr from 1956 to 1973.

growth rate in the 1920s was similar to the growth observed in recent years.

Several observations suggest that growth of walleye in the lake is a function of prey density. One line of evidence is the close relation between length increments of age I–IV walleye and indices of young perch abundance in 1961–69 (Fig. 6). Biomass of young perch taken in trawls on August 1 plus production by the cohort between August and October was calculated as an index of perch biomass available to walleye (Forney 1971). A strong growth response to variation in perch abundance would be expected because young perch comprised 70–98% of the identifiable fish in stomachs of walleye and were consistently the most abundant species in trawl catches.

Differences in seasonal growth patterns of walleye in 1971, when young yellow perch were abundant, and in 1973, when young white perch were numerous, reinforced the conclusion that prey density regulated growth. Mean weights of age III walleye captured in trawls fished at depths of 6–10 m near Shackelton Point in 1971 increased rapidly in July and slowed markedly in September (Fig. 7). This pattern of weight gain was characteristic of years in which young yellow perch were abundant. Walleye subsisted on yearling perch and invertebrates in the spring of 1971 and shifted to young perch in mid-June, when the perch cohort had attained a mean length of about 18 mm (Forney 1974). Growth in weight could not be detected before mid-June, although water temperatures at 10 m exceeded 12°C, the physiological threshold for growth (Kelso 1972), by mid-May. Apparently the food supply was inadequate to sustain growth until augmented by young perch. Young perch predominated in the diet of walleye and trawl catches, and growth of walleye terminated in early October as perch abundance declined.

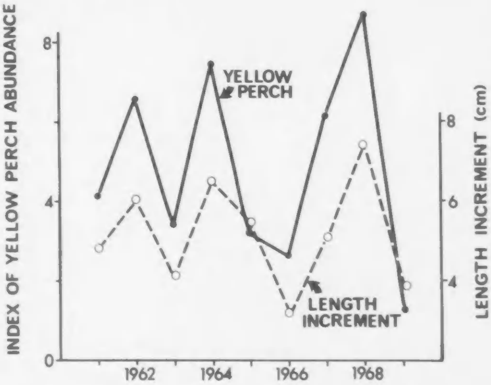

FIG. 6. Mean annual length increments by age I–IV walleye in 1961–69 vs. biomass of age 0 perch on August 1 plus production from August to October estimated from trawl catches.

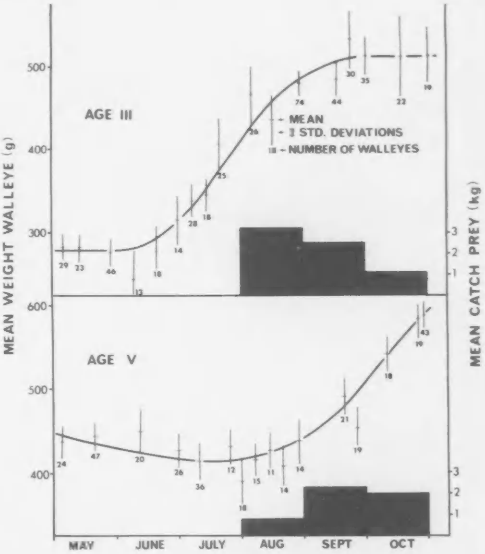

FIG. 7. Seasonal trends in observed weight of age III walleye in 1971 and age V walleye in 1973 captured in trawls, and (bars) mean monthly catches of forage-size fish in trawls in August–October.

A different pattern of prey abundance and growth was observed in 1973. The catches of young perch in trawls averaged 381 per haul in early August 1973, compared with over 3000 in 1971. As expected, walleye consumed fewer young yellow perch in 1973 than in 1971, and apparently food intake was inadequate to meet maintenance requirements of age V walleye, since their mean weight declined through July (Fig. 7). Younger age-groups showed a similar trend but the weight loss was less pronounced. Walleye did not show a weight gain until August and the rapid increase in weight of age V walleye in September and October was paralleled by a rise in consumption of white perch. In contrast to yellow perch, the hatch of white perch was highly successful (Table 1) and the biomass of forage-size fish in trawls rose in late summer with the transition of white perch from the pelagic to demersal mode. Walleye were able to capitalize on a food supply that was not available in 1971 and growth accelerated in the fall of 1973.

The close relation between walleye growth and annual and seasonal variation in prey abundance is interpreted as evidence of severe food competition. Walleye and other piscivorous species apparently consumed a high proportion of the annual prey production during a short time interval and weight gain by walleye was restricted to a segment of the potential growing season (Fig. 7). The result was a relatively slow annual growth rate and small adult size.

The stable size composition of the adult stock and absence of any long-term trend in growth rates implies that the walleye population has been in equilibrium with its food supply since the early 1940s and probably longer. Growth homeostasis may be explained by the concomitant response of growth and recruitment to variation in prey abundance. Strong year-classes of walleye usually develop in years when growth is rapid (Fig. 8) because high prey density, which enhances growth, also reduces cannibalism by adults on age 0 walleye (Chevalier 1973; Forney 1974). As biomasses of successful year-classes increase through growth, intraspecific competition for food should intensify and growth rates decrease. Simultaneously, intraspecific competition would intensify cannibalism and survival of succeeding year-classes of walleye would be suppressed. This scenario, repeated over a period of years, would adjust walleye growth to prey production, although time lags and random environmental perturbations would induce instability in annual growth and recruitment.

General Discussion

The nature of competition between walleye and other predators in the early 1900s must be inferred from contemporary knowledge of species interactions. Broad overlap in diets of most piscivorous fish (Scott and Grossman 1973) suggests that eel, esocids, and walleye probably shared a common food resource. Whether this food resource was limited in unknown, but the small egg complement of females (Fig. 4) indicates walleye matured at a small size and possibly were food limited at a time when eel and esocids were common. As eel and esocids declined and interspecific competition relaxed, the number of walleye rose (Fig. 3). Although there was no evidence of an increase in average size of walleye, the absence of a growth response may be explained by the rise in walleye biomass. Thus, a reduction in interspecific competition with eel and esocids for food was likely counteracted by an increase in intraspecific competition.

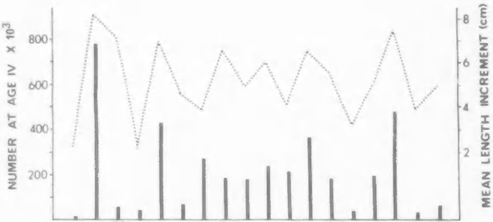

FIG. 8. Mean annual length increments of age I–IV walleye in 1954–70 (dotted line) and mark–recapture estimates of numbers of walleye hatched in the various years that survived to age IV.

The transition from a diverse predator population to one dominated by walleye did not seriously disrupt the community. Although some cyprinids declined, centrarchids showed little change in abundance and yellow perch retained a position of dominance. However, the shift in predator composition in the 1920s and 1930s may have induced changes in size composition of the perch population. Most yellow perch caught by anglers in 1916–27 were <20 cm (W. A. Dence personal communication) but by the 1950s the majority of yellow perch in the angling catch and in experimental gear were 23–30 cm with few under 20 cm. Scales and measurements from perch collected in 1916–27 by Adams and Hankinson (preserved specimens from the Roosevelt Wildlife Collections, Syracuse University) confirm that age I and II perch were smaller than those perch produced in recent years (Fig. 9).

The smaller size of perch in 1916–27 may have resulted from a temporary disturbance of predator–prey relationships which led to overpopulation and reduced growth. Perhaps equally plausible is that the decline in esocids and increase in the walleye population during the 1930s shifted predation from older to young age-groups, which enhanced growth of perch. Walleye may deplete yellow perch cohorts more rapidly than esocids, which are less likely to invade the pelagic region and also tend to consume larger prey and consequently fewer prey per kilogram body weight. Le Cren et al. (1972) presented a similar argument to explain the increased growth and average size of *Perca fluviatilis* in Lake Windermere following a reduction in average size of northern pike.

Much of the instability in walleye recruitment and growth is linked to variation in prey abundance. The walleye in Oneida Lake is highly dependent on young perch as forage and alternative prey are either scarce or unavailable (Forney 1974). Fluctuations in walleye stock are further magnified by variation in vulnerability of walleye to exploitation, which is also linked to prey abundance (Forney 1967; Kempinger et al.

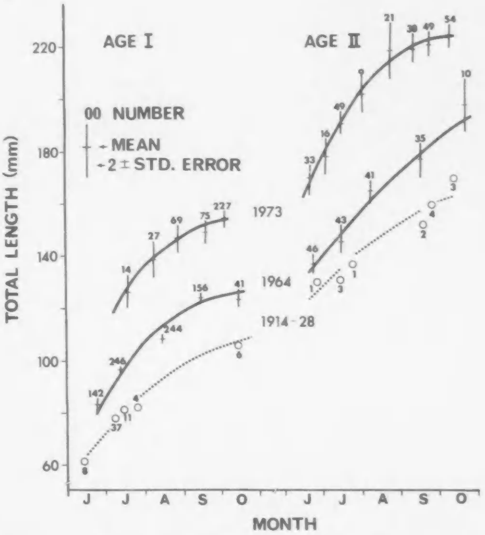

FIG. 9. Observed lengths of age I and II yellow perch collected in 1914–28, and lengths of perch from the 1964 and 1973 year-classes. Mean lengths of other year-classes produced in 1962–74 fall within the ranges depicted by the 1964 and 1973 year-classes.

1975). Apparently the walleye population, and by implication prey abundance, varied less in the 1930s, when walleye and esocids were codominant predators. The increase in CPE of spawning females at Scriba Creek was matched by an equally marked increase in annual fluctuations in CPE (Fig. 1). Though the argument that a more diverse predator population would generate a more diverse prey population is appealing, seine catches in 1916–27 and 1960–70 did not reveal a marked change in species competition. However, smaller size of yellow perch may have enabled walleye to prey on several age-groups of perch, thus reducing dependency on success or failure of a single year-class.

The composition and structure of the Oneida Lake fish population is largely a fortuitous outcome of man's activities. Canalization, destruction of wetlands, and probably less easily identified cultural changes nearly eliminated eel and esocids, and walleye have flourished. The transition was orderly and yellow perch remained an important link in the transfer of energy from secondary to higher trophic levels. The reduction in predator diversity has enhanced the economic value of the fishery, since the walleye is the preferred sport fish, but wide fluctuations in recruitment of walleye suggest that the simplified walleye–yellow perch association is less stable.

Acknowledgments

Federal Aid in Fish and Wildlife Restoration funds through the New York State Department of Environmental Conservation have provided continuous support for fisheries studies on Oneida Lake since 1957. I thank Herbert Lake for Oneida Hatchery reports, R. Werner and A. Marsters for providing access to the Roosevelt Wildlife Collection, and M. D. Clady for his comments on an earlier draft of this paper.

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Changes in Yellow Perch (*Perca flavescens*) Populations of Lake Michigan, 1954–75[1,2]

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WELLS, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954–75. J. Fish. Res. Board Can. 34: 1821–1829.

In the early and mid-1960s the abundance of yellow perch (*Perca flavescens*) in Lake Michigan declined abruptly. The decline began in the northern part of the lake and spread progressively southward. Circumstantial evidence suggests that the nonnative alewife (*Alosa pseudoharengus*), by interfering with perch reproduction, was the primary cause of the decline. The alewife was first reported in northeastern Lake Michigan in 1949, and had become extremely abundant throughout the lake before an enormous die-off in 1967 reduced its numbers by an estimated 70%. An intensive fishery hastened the decline of perch. In most areas the decline was immediately preceded by a period of conspicuously high commercial production. This high production appears to have been related in part to increased growth rates of perch resulting from much lower density of younger fish. A sport fishery for perch in shallow water collapsed a few years before the species declined in abundance. The most logical explanation is that heavy concentrations of alewives physically displaced the perch from nearshore areas. Although perch populations increased in some areas in the 1970s, a full recovery is unlikely unless alewife numbers are further reduced.

Key words: Percidae, Lake Michigan, *Perca*, population dynamics, exploitation, competition

WELLS, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954–75. J. Fish. Res. Board Can. 34: 1821–1829.

Au début et au milieu des années 1960, il y eut déclin abrupt de la perchaude (*Perca flavescens*) dans le lac Michigan. Commençant à la partie nord du lac, le déclin s'étendit progressivement vers le sud. Des preuves indirectes suggèrent que le gaspareau (*Alosa pseudoharengus*), espèce non indigène, fut la cause principale du déclin en nuisant à la reproduction de la perchaude. On a signalé le gaspareau pour la première fois dans le nord-est du lac Michigan en 1949, et l'espèce était devenue extrêmement abondante dans tout le lac avant que des mortalités en masse en 1967 en diminuent le nombre d'environ 70%. Une pêche intensive hâta le déclin de la perchaude. Dans la plupart des régions, le déclin fut précédé d'une période de très forte production commerciale. Cette forte production semble liée en partie à des rythmes de croissance plus rapides chez la perchaude, résultant d'une densité beaucoup plus faible de jeunes poissons. Une pêche sportive de la perchaude en eau peu profonde s'affaissa quelques années avant le déclin de l'espèce. L'explication la plus logique est que les fortes concentrations de gaspareaux déplacèrent physiquement les perchaudes des régions littorales. Bien que les populations de perchaudes aient augmenté dans certaines régions pendant les années 1970, il est peu probable qu'il y ait rétablissement complet à moins que l'abondance du gaspareau ne soit réduite davantage.

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IN this paper I describe changes that have occurred in yellow perch (*Perca flavescens*) populations of Lake Michigan during the period 1954–75, and present my views on the reasons for the changes. The subject was previously discussed briefly by Smith (1970) and Wells and McLain (1973). The present report contains data not included in the earlier reports, and expands considerably the analyses and discussion.

The yellow perch in Lake Michigan has been important as a commercial species since the 1880s, and as a sport fish since at least the 1920s. Annual commercial production has usually fluctuated between 0.5 and 1.5 million kg (Baldwin and Saalfeld 1962 plus Supplement 1970). The

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Contribution 529 of the Great Lakes Fishery Laboratory.

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annual take by anglers may often have consisted of millions of fish, judging by limited catch data compiled since 1970.

Primary sources of data for this report are the commercial and sport fisheries, and survey (experimental) fishing. The data from all sources contain notable shortcomings. Consequently, in their interpretation I often was forced to resort to speculation. Nevertheless, I am confident that my appraisal of the changes in the Lake Michigan perch populations is generally sound.

Lake Michigan is divided among four states — Michigan, Wisconsin, Illinois, and Indiana (Fig. 1) — each of which exercises complete jurisdiction over waters within its borders. The greatest shares by far belong to Michigan and Wisconsin. Lake Michigan's length is 494 km, its maximum width 190 km, its surface area 58,200 km^2 (sixth largest freshwater lake in the world), its mean depth 84 m, and its maximum depth 281 m. An environmentally distinct part of the lake, Green Bay, which is 190 km long and averages 37 km in width, is generally more eutrophic and productive than the main lake. The biota of Lake Michigan is generally typical of that of North American oligotrophic lakes. Many species of flora and fauna characteristic of less oligotrophic situations (e.g. the yellow perch) are also common, however, particularly in nearshore waters and in Green Bay. A more detailed description of the lake was given by Wells and McLain (1973).

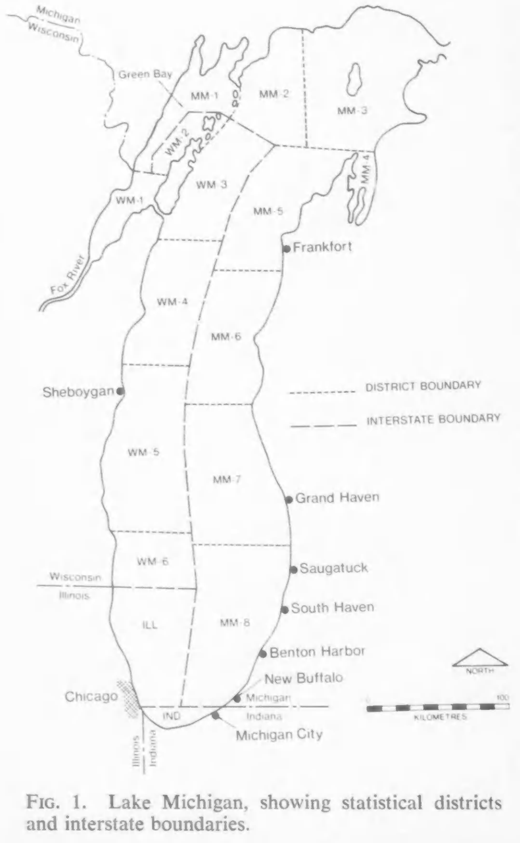

FIG. 1. Lake Michigan, showing statistical districts and interstate boundaries.

Distribution of Perch in Lake Michigan

Yellow perch are distributed throughout Lake Michigan where depths are suitable. Commercial catch records indicate that abundance has ordinarily been greatest in Green Bay and in the southern part of the lake. Perch in Lake Michigan are mainly demersal, although some occupy mid-levels in summer (Wells 1968).

In southeastern Lake Michigan, postlarval young-of-the-year (hereafter referred to as "young") live mostly in depths less than 5 m until fall; in October and November they are most numerous at depths of 13–22 m but have been found as deep as 31 m (unpublished data, Great Lakes Fishery Laboratory [GLFL]). After their first year they are mainly at depths of 9–27 m in winter and early spring; less than 18 m in late spring and early summer; less than 27 m in late summer; and 18–37 m in fall (Wells 1968; unpublished data, GLFL). In summer, perch are often concentrated in a relatively small interval within the depth ranges given, and the depth of greatest abundance may shift rapidly as bottom temperatures fluctuate.[3]

Catches of Yellow Perch: Commercial, Sport, and Survey

Commercial catches — Commercial catch data are from reports that each fisherman is required to submit monthly to the state in which the fish are caught. Although the commercial statistics used in this report, i.e. total catches and catches per unit of effort (CPEs), do not reflect abundance precisely, they nonetheless provide a useful basis for estimating major changes and trends in yellow perch populations.

For indicating changes in perch populations, annual commercial catches for individual statistical districts are more meaningful than are annual figures for the entire lake. Statistical districts of Lake Michigan (Fig. 1) are designated as MM-1 to MM-8 in Michigan waters, and WM-1 to WM-6 in Wisconsin; Illinois and Indiana each have one district. The production figures presented here refer only to perch caught in small-mesh gill nets (5.4- to 7.6-cm mesh, extension measure). I ignored the catches in other gear, which were insignificant except in southern Green Bay (WM-1), to simplify comparisons. Data were combined for two or more districts in which trends were closely similar, e.g. all districts of Green Bay (Table 1).

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[3] On the basis of a scarcity of young and yearling perch in trawl collections made entirely at depths of 5 m and more in Lake Michigan in 1964, I assumed (Wells 1968) that most perch of these ages in the lake live at depths less than 5 m. Regrettably, my interpretation of the data was inaccurate for young in the fall, and generally incorrect for yearlings — the perch population at that time simply contained few young and yearlings.

In the lake proper, production in all districts fluctuated without conspicuous trend from 1954 to 1959, although year-to-year changes were occasionally considerable. Catches declined sharply in all areas in the early or mid-1960s. The decrease was preceded in most districts by a period of increased fishing effort (as can be computed from the data in Table 1) and production. In the southern districts, CPEs were high in the year of highest production, or the year before. The decline began earlier in the northern than in the southern areas. Catches began dropping in 1961 in northern districts MM-2, 3, and 4 and WM-3 and 4; in 1962, farther south in district MM-5; and in 1965 in the rest of the districts. Production in 1965 was meager in all districts except MM-8, and had not recovered significantly in Michigan by 1969 (the last year in which commercial fishing was allowed), nor in Wisconsin by 1975. Catches increased in Illinois and Indiana in 1971 and 1972, but then declined.

In Green Bay, the most notable features of the commercial catches from 1954 to 1975 were: a period of high production from 1960 to 1963, accompanied by high CPEs in 1962 and 1963; a precipitous decline from 1964 to 1966; and temporary sharp increases in 1967 and 1974 (Table 1).

Sport catches — Published data pertaining to the sport fishery are scanty, and the information I obtained was largely through personal communications. The yellow perch evidently supported a highly important sport fishery in Lake Michigan in the middle 1950s, as it had for many years before. Long-time residents around the lake stated that large numbers of anglers fished from every breakwall; some also fished from boats in shallow, protected areas, particularly in Green Bay. (Angling from boats became popular in some open-water areas in the 1970s.)

A rather sudden decline in the sport fishery for perch began in the late 1950s. The exact years are difficult to determine, but they were definitely earlier than those in which the commercial fishery declined in corresponding parts of the lake. Apparently the last year of good angling before the collapse was 1958 in northern Green Bay, 1959 at Grand Haven in the southeastern part of the lake, and 1960 at Sheboygan, in the west–central part of the lake.

A partial recovery of the sport fishery took place in much of the lake beginning about 1970. Results of a mail survey conducted by the State of Michigan each year from 1970 to 1975 indicate that the catch increased steadily during that period, and may have been about 2 million fish in State of Michigan waters alone in 1975 (G. C. Jamsen, Michigan Department of Natural Resources [DNR], personal communication). Largest numbers were taken in the southeastern part of the lake and in northern Green Bay. Creel census data for Indiana waters suggest that the catch may have been as high as 200,000 fish in 1975, but this total was noticeably less than that in 1973 (R. A. Koch, Indiana DNR, personal communication). The improvement in sport catch apparently was not as great in Illinois waters, and particularly in Wisconsin waters of the lake proper, as in some other parts of the lake. In Wisconsin waters of Green Bay, however, a sizable sport fishery developed in late 1973 and continued through 1974, but declined markedly in 1975 (R. W. Langhurst, Wisconsin DNR, personal communication).

Survey catches — Experimental data were collected with bottom trawls from the U.S. Fish and Wildlife Service research vessel *Cisco*. All collections were made in the fall in Michigan waters of the southeastern part of the lake, off Saugatuck and, 51 km to the north, Grand Haven (Fig. 1).

Data from Saugatuck were collected in standardized series of tows each year from 1962 to 1975. Each series consisted of 10-min tows with a trawl having a headrope of 11.9 m and cod-end mesh of 1.3 cm (extension measure), fished along the contour at 14 depths between 5 and 92 m. (Nearly all the yellow perch in the collections came from depths of 13–37 m.) Young, yearlings, and older perch (hereafter referred to as "adults") in the catches are considered separately. Data from Grand Haven are limited to a few scattered collections in 1954 and 1960.

In the survey catches off Saugatuck, adults declined sharply in 1964 and never recovered; yearlings and young were scarce in all years except 1970, when young were moderately common (Table 2). No yearlings were taken from 1964 to 1966, and no young from 1963 to 1965. Al-

TABLE 1. Commercial production (thousands of kg) of yellow perch, and catch per unit of effort (CPE in kg per 672 m of gill net of mesh sizes 5.4–7.6 mm, extension measure) in various statistical districts of Lake Michigan. (See Fig. 1 for locations of districts. The commercial fishery was closed in State of Michigan waters in 1970–75.)

	MM-2, 3, 4		WM-3, 4		MM-5		MM-6, 7		MM-8		WM-5, 6		Illinois		Indiana[c]		Green Bay	
Year	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE
1954	21	28	47	31	4	44	135	66	133	71	146	50	91	55			221	31
55	41	35	98	54	4	36	93	59	128	63	251	79	164	62			295	39
56	31	47	104	46	5	68	108	66	141	55	230	69	103	60			306	42
57	28	48	90	60	7	80	74	56	49	38	347	81	96	58			315	41
58	39	37	148	44	7	31	80	53	106	40	406	58	106	62			377	41
59	32	43	80	44	10	22	39	57	61	47	120	52	55	91			277	56
1960	69	45	127	52	26	55	57	51	71	40	343	72	87	105			514	53
61	54	29	118	45	58	32	76	63	167	56	645	88	79	89			729	52
62	10	22	54	53	20	40	90	63	141	71	408	98	101	101			613	78
63	5	17	48	62	15	38	108	76	111	77	760	141	99	103			679	84
64	7	23	20	29	23	55	176	48	740	83	765	73	280	80			392	40
65	1	19	5	16	2	17	34	27	281	49	67	26	50	49			77	17
66	1	9	1	12	1	18	11	21	142	45	34	25	14	22			34	19
67	—[a]	4	1	24	1	13	8	26	160	57	27	31	3	25			200	40
68	—[a]	1	—[a]	4	0[b]	—	4	27	65	52	12	34	32	70			79	23
69	1	9	—[a]	1	—[a]	8	2	14	97	65	16	37	24	60			74[d]	28
1970			—[a]	5							27	36	25	73	90	55	76	27
71			—[a]	19							25	31	47	66	150	57	47	19
72			2	20							40	40	154	57	164	90	41	19
73			7	20							25	26	83	52	117	49	39	19
74			7	15							11	17	128	52	81	29	200	44
75			13	17							11	15	70	27	42	41	101	17

[a] Less than 500 kg.

[b] No effort.

[c] Data incomplete before 1970.

[d] Catches in State of Michigan waters of Green Bay in 1969 made up only 16% of the total for Green Bay.

TABLE 2. Numbers of adult, yearling, and young-of-the-year yellow perch caught in standard series of trawl tows[a] in various years off Saugatuck, Michigan. (Numbers for 1969 and 1970 are averages for three standard series and those for 1971 for two.)

Year	Adults	Yearlings	Young-of-the-year
1962[b]	249	43	3
1963	599	39	0
1964	91	0	0
1965	24	0	0
1966	18	0	21
1967	41	1	7
1968	23	3	3
1969	1	0	7
1970	15	40	81
1971	17	9	5
1972	13	13	4
1973	15	1	8
1974	11	27	30
1975	41	59	33

[a] See text for description of standard series of tows.

[b] One tow of the standard series, at 22 m, was omitted in 1962.

though the catches of adults appeared to increase notably from 1962 to 1963, the comparison is made less reliable by the omission in 1962 of a normally productive tow at a depth of 22 m — a tow which in 1963 took 73% of the adults and 69% of the yearlings for the series (unpublished data, GLFL).

Catches at Grand Haven in 1954, in 10-min tows with trawls similar to those used at Saugatuck, were occasionally much larger than any made later at Saugatuck. Examples of large catches in 1954 were 2,041 yearlings and adults (combined) in a tow in November; 202 yearlings and 480 adults in a tow in December; and a total of 245 young in three consecutive tows in November.

The catches at Grand Haven in 1960 serve only to suggest that a standard series at that time would have produced at least fairly large catches of adults and yearlings, and that the ratio of yearlings to adults would have been higher than in 1962, and particularly 1963. Ten-minute tows at each of four depths between 18 and 46 m, with a trawl somewhat larger than those used at Saugatuck, yielded 353 adults and 117 yearlings. The cod-end mesh (4.1 cm) of the net was probably too large to retain young.

Fluctuations in Perch Populations

Commercial catches per unit of effort indicate that perch populations declined in all areas of the lake in the early and mid 1960s, that the decline was preceded in southern areas and Green Bay by an increase in abundance, and that the decline occurred first in the north. The limited data from the sport fishery support the occurrence of a lakewide decline spreading from north to south, but suggest that it might have begun earlier than indicated by the commercial catches. Survey data suggest that numbers of smaller fish decreased before commercial production gave any indication of a decline. The following more detailed discussion of these changes pertains chiefly to the southeastern part of the lake where all experimental data were collected; however, the general conclusions should apply to other parts of the lake as well.

The scarcity of young and yearlings in the experimental catches of 1962 and 1963 indicated that the decline resulted primarily from low reproduction. The larger numbers of adults in 1954 than in 1962 suggested that reproduction began to diminish several years before 1962. Judging by the relatively large catch of yearlings in 1960, as compared with 1962, reproduction was greater in 1959 than in 1961; however, the data do not permit a comparison of the 1959 year-class with those in earlier years. Reproduction was extremely deficient in 1963–65. The sharp decline in adults in the survey catches in 1964 is not incompatible with the high commercial production in that year; most of the commercial catches were made before the experimental sampling in the fall. The poor experimental catches in the fall accurately foretold the much lower commercial production that followed in 1965.

Catches per unit of effort in the commercial fishery did not reflect the changes in abundance of adults between 1954 and 1962 that was indicated by the experimental catches. The CPEs in MM-8 were as high in 1962 as in 1954 (Table 1) despite the decline in adults, principally because the proportion of the adult population above the minimum legal size limit of 216 mm, i.e. the segment within the commercial size range, was much greater in 1962 than in 1954. In the survey catches, fish 216 mm long and longer constituted only 1.4% of the adults in 1954, compared with 45% in 1962. The difference in proportion of larger fish was partly due to changes in age structure — only 29% of the adults were age III and older in 1954, compared with 77% in 1963 (data for 1962 not available) — but also partly to changes in growth rates. In fish from experimental samples (not previously mentioned in this report, except those of 1954) growth rates in-

TABLE 3. Average total length (mm) of male and female yellow perch of different ages caught in bottom trawls in southeastern Lake Michigan[a] in various years. (Since all fish were sampled between growing seasons, lengths represent the lengths at the completion of the indicated number of growing seasons. Calendar years indicated refer to the respective growth years most recently completed, even though the collection may have not been made until the following spring. Categories represented by less than four fish were not considered.)

Most recent growth year, and sex	Number of fish	Growing seasons completed						
		2	3	4	5	6	7	8
1954								
Male	228	128	154	175	188	193		
Female	167	126	163	189				
1963								
Male	28		175	191	206	218		
Female	20		188	203				
1964								
Male	84	154	185	204	217			
Female	73	156	202	222				
1970								
Male	31	177	210	233	258			
Female	19	176		267	290			
1975								
Male	152		199	229	248	264	278	
Female	107		218	241	280	308	331	348

[a] Collections were from Grand Haven in 1954; Saugatuck in 1963, 1964, and 1970; and Grand Haven, Saugatuck, and South Haven combined in 1975.

creased between 1954 and 1963, were even greater in 1964, and were greater still in 1970 (Table 3). The increase between 1963 and 1964, which almost equaled that in the 9-yr span between 1954 and 1963, suggests that the more rapid growth began only a few years before 1963. The increased growth seems likely to have been related to declining abundance — i.e. decreasing total numbers of all perch, including those under commercial size. It is improbable that an increasing abundance of food organisms was the cause, since faster growth occurred without regard to age, and it is doubtful that the food of both smaller and larger perch would have become more abundant. The increasing CPEs between 1960 and 1964 in district MM-8 (Table 1) may have resulted from fish reaching commercial size at progressively earlier ages, and from fish of increasingly larger average size in the catches — rather than from an actual increase in the number of adult perch in the population.

Indirect evidence suggesting that increases in production and CPE of perch were taking place concurrently with a decline in abundance is provided by data that demonstrate convincingly that just such an event did occur in another Lake Michigan species — the bloater (*Coregonus hoyi*) — only a few years later (Brown 1970; unpublished data, GLFL). Decreasing strengths of year-classes beginning at least as early as the middle 1960s (probably sooner) was accompanied by increased growth rates. As the fish became larger, commercial production and CPE (but not effort) climbed rapidly. Coincidental with those increases were declines in the actual numbers of bloaters in the populations. Finally, in 1970, a rapid decline in production began and continued without letup.

The collapse of the sport fishery for perch in the southeastern part of the lake in about 1960, when the species was still at least fairly abundant, appears to have been related to changes in depth distribution of perch, or perhaps other factors (discussed later).

Survey data from Saugatuck indicated that perch reproduction in that area improved somewhat after 1965, although they gave no indications of the development of very strong year-classes. The abundance of adults remained low after 1964, at least in the smooth-bottom areas in which the survey trawling was conducted.

The trawl catches at Saugatuck in the 1970s failed to reflect the increase in adults in the southeastern part of the lake that was indicated by the increase in sport catches starting about 1970 (described earlier), and by a decrease in growth rates between 1970 and 1975 (Table 3). The increase in abundance resulted in part from a strong year-class that was produced in 1969 in at least the extreme southeastern portion of the lake. A standard series of trawl tows in the fall of 1969 at Benton Harbor, 65 km south of Saugatuck, took 236 young, as compared with a range of only 4–59 in similar series conducted each year from 1967 to 1975 (unpublished data, GLFL). The year class was further represented by large catches of yearlings in trawls at Benton Harbor in 1970, and adults in experimental gill nets in east–central, southeastern, and extreme southern parts of the lake in 1971–75 (unpublished data, GLFL; Brazo et al. 1975; Patriarche 1975; M. C. Cochran, NALCO Environmental Sciences, Northbrook, Illinois, personal communication).

The scarcity of young in 1969, and of yearlings in 1970, in the trawl catches at Saugatuck (Table 2) suggests that the strong reproduction may have been limited to an area south of Saugatuck, and that many of the adults of the 1969 year-class caught in the gill nets in the area off Saugatuck and northward may have been immigrants. Data are not available to show the southern limit of the area of high reproduction in 1969. Although the 1969 year-class was well represented as adults in gillnet catches, it was not taken in large numbers in catches of adults in trawls at either Benton Harbor or Saugatuck. A possible explanation for this apparent anomaly is that adult perch in the 1970s (and probably late 1960s) were usually concentrated over bottoms too rough for bottom trawling. When identical gill nets were fished periodically in 1974 on sandy and rocky bottoms near Saugatuck, many more perch were usually taken in the rocky than in the sandy area (unpublished data, GLFL). Evidently, after the decline, adult perch were distributed only over their preferred bottom, and perhaps would have had to increase in abundance substantially before they filled this habitat and spread into all the areas they occupied before the decline. Modest changes in adult populations might not greatly affect abundance on smooth bottoms, and therefore could go undetected in bottom-trawl catches.

High commercial production in Illinois and Indiana in 1971 and 1972 probably reflected primarily the strong 1969 year-class — just as the increased commercial catches in southern Green Bay in 1974 resulted from strong year-classes in 1971 and 1972 (R. W. Langhurst, personal communication).

Factors in Population Changes

The described changes in Lake Michigan yellow perch populations were almost unquestionably caused primarily by the invasion and population explosion of the alewife (*Alosa pseudoharengus*), a nonnative species. An intensive commercial fishery also played a role. The sport fishery probably had some influence in the more recent years. Habitat deterioration seems not to have been a factor.

Effects of the alewife — The first alewife reported from Lake Michigan came from the northeastern part in 1949 (Miller 1957). By 1953 at least a few alewives had dispersed throughout most of the lake, and they were common in Green Bay. Large numbers of young were observed in the northern region of the main lake in 1955, and the species became common in the southern region by the winter of 1956–57. Thereafter alewives proliferated rapidly until an enormous die-off in 1967 reduced their abundance by an estimated 70% (Brown 1972; unpublished data, GLFL). The population began a recovery in 1969, but numbers remained considerably lower than those of the mid-1960s. (For further details of alewife population changes in Lake Michigan, see Miller 1957; Brown 1972; and Wells and McLain 1973.)

I base my conclusion that the alewives have greatly affected perch primarily on the coincidence of the alewife population buildup and the changes in perch populations. Several changes in Lake Michigan besides those involving perch populations occurred more or less simultaneously during the alewife population increase, suggesting that all resulted from the same cause and that the most likely cause was the alewife. Among these changes were a marked decline in large zooplankters as alewives became abundant, and partial recovery after the alewife die-off of 1967 (Wells 1970); and conspicuous decreases in populations of bloaters (described earlier) and emerald shiners (*Notropis atherinoides*). Emerald shiners were once so abundant in Lake Michigan that they occasionally clogged the intake screens of water filtration plants (Flittner 1964). Although their life history is poorly known, evidently they occupied shallow areas, including harbors, except during summer when they were pelagic. Emerald shiners declined suddenly, apparently in the north first. They became rare in northern Green Bay in the mid-1950s (E. Apelgren, Bay de Noc Lure Company, Gladstone, Michigan, personal communication) and in the southern part of the lake in the early 1960s (Wells and McLain 1973); they later recovered only slightly, if at all.

The data suggest that the alewives interfered with the reproduction of perch. Reproduction of perch was weak in southeastern Lake Michigan in the early 1960s, when the alewife was abundant, and it is significant that perch produced a strong year-class in the extreme southeastern part of the lake in 1969, when alewife abundance was relatively low.

Detrimental effects by alewives on yellow perch reproduction can easily be conceived. Alewives move shoreward in spring (Wells 1968) and are heavily concentrated in perch spawning and nursery areas during the reproductive season of perch. The exact nature of the interference, however, is not clear. Commercial fishermen consider that when alewives became abundant, perch began spawning in deeper waters than formerly — a change which may have been injurious to reproduction, particularly if the deeper areas lacked adequate materials for attachment of eggs. No evidence exists, however, to confirm or repudiate the fishermen's view that spawning sites were shifted. The eggs themselves probably did not suffer directly from alewives — at least they evidently are not eaten by alewives, perhaps because they are protected by the gelatinous material in which they are embedded (Wells and McLain 1973).

The greatest damage to perch by alewives may come at the larval stage of the perch. Predation on the larvae by alewives seems a distinct possibility, although evidence for such feeding is lacking. No fish larvae of any species have been found in stomachs of Great Lakes alewives (e.g. Morsell and Norden 1968; Price 1963) except for unidentified larvae in a single fish from Green Bay (Gannon 1972) and alewife larvae in a substantial portion of alewives in a sample collected in the extreme southern part of Lake Michigan in the fall (Rhodes et al. 1974). Although the food studies suggest that fish larvae are not common in the diet of alewives, the evidence that this is a fact is not conclusive. Tests conducted at GLFL indicate that fish larvae eaten by alewives may easily go undetected in food studies because they are rapidly digested beyond recognition (T. A. Edsall, GLFL, personal communication). In any case, adverse effects by alewives on perch larvae would not necessarily need to be explained by predation. Competition for food, or other relations less readily envisoned may be involved.

The alewife must have been instrumental in the peculiar lakewide collapse of the sport fishery for perch at a time when the perch were still abundant. Two explanations for the relation have been commonly proposed. Although neither appears wholly satisfactory, the seemingly most creditable one, and one subscribed to by many biologists (e.g. Smith 1970) and a few fishermen, is that the perch refused to enter the very shallow waters (where most angling was done) when alewives became massed there in heavy concentrations. This hypothesis is supported by reports from commercial fishermen that they were required to move their nets into deeper water than formerly to catch perch successfully after alewives became abundant. Nevertheless, experimental trawls fished from the R/V *Cisco* at Saugatuck in 1964, some years after the decline of the sport fishery, occasionally took large numbers of perch in spring and summer in the shallowest area sampled, i.e. 5 m (Wells 1968) — little deeper than the water near the ends of the breakwalls. Perhaps the physical displacement of perch by alewives occurred only where the alewives were extremely concentrated in spring and early summer for spawning. Alewives in Lake Michigan spawn mostly in streams and protected areas, including harbors, and consequently are heavily concentrated near breakwalls and in bays during the spawning season.

Many anglers believe that sport fishing for perch declined because the reason (as perceived by the anglers) for the perch coming into the shallow waters in bays and around breakwalls, i.e. to feed on emerald shiners, ended with the disappearance of the shiners — a relation which, if true, would have implicated the alewife indirectly. Certain events tend to discredit this hypothesis, however. For example, the failure of the sport fishery does not appear to have coincided exactly with the near-extermination of the shiner: anglers in northern Green Bay took perch successfully in the mid-1950s, when shiners there were already scarce (E. Apelgren, personal communication); and sport fishing for perch in the southeastern part of the lake (at least off Grand Haven) was poor by 1960, when emerald shiners in the area were still abundant. Furthermore, a considerable improvement in angling from the breakwalls in the lake proper and from boats in some of the protected areas of northern Green Bay took place in the 1970s without a corresponding resurgence of emerald shiner populations.

Effects of the fisheries — Although data on which to base firm conclusions are lacking, there seems little doubt that intensive fisheries (mainly commercial) hastened the declines of perch populations in Lake Michigan in the 1960s. An abrupt decline of adults such as that indicated by the drop in survey catches from 1963 to 1964 in the southeastern part of the lake, for example, was unlikely to have occurred entirely from natural causes. Sport and commercial fishing each were intensive enough in the 1970s to affect perch populations in certain areas. The sport fishery in 1975, for example, took an estimated 500,000 perch in State of Michigan waters of Green Bay (G. C. Jamsen, personal communication) and, as reported earlier, 200,000 in Indiana waters. Although the estimates are subject to considerable sampling error, they nevertheless suggest that anglers in those areas took some significant portion of the perch population.

Outlook

The abundance of yellow perch in Lake Michigan in the future probably will depend to a considerable extent on the density of alewives. Alewife abundance showed signs of stabilizing in the early 1970s at a level somewhere between the abundance before and after the die-off of 1967. Perhaps alewives are prevented from regaining their former abundance by predation losses to several species of salmonids such as lake trout (*Salvelinus namaycush*), coho salmon (*Oncorhynchus kitsutch*), and chinook salmon (*O. tschawytscha*). Large numbers of salmonids have been stocked in Lake Michigan in recent years, e.g. about 11 million in 1975 (A. K. Lamsa, Great Lakes Fishery Commission, personal communication), and are known to prey heavily on alewives (unpublished data, GLFL). If salmonids are making inroads into alewife populations, and salmonid stocking rates increase in the future — as seems likely — alewife populations may decrease to the extent that perch can proliferate greatly. If, on the other hand, alewives do not decline through one means or another, it is improbable that perch will regain their former abundance. It may be added that it is highly doubtful that alewives will be permitted to decline seriously if such a decrease can be avoided, because fishery managers consider the alewife essential to the successful salmonid programs in Lake Michigan.

Perch in Green Bay, particularly in the southern portion, will probably fare better than in the lake proper if alewife numbers do not diminish. Strong year classes were produced in southern Green Bay (and perhaps the northern part as well) in 1971 and 1972, as mentioned earlier, and in 1975 (M. Hawley, Wisconsin DNR, personal communication). The marshy habitat along the edges of some parts of Green Bay (but lacking in the lake proper) may offer spawning and nursery grounds relatively free from interference by alewives. Southern Green Bay also has a possible advantage in the relative dates of perch spawning and the appearance of large concentrations of alewives. Perch spawning occurs earlier, and alewife concentrations later, than in the lake proper, and consequently alewives may be less likely to interfere with perch reproduction.

Perch populations in future years may be influenced by the magnitude of the harvest. The commercial fishery, where it is allowed, is intensive, and the sport fishery appears to be reaching major proportions. Management agencies may need to consider controlling the harvest through such means as imposing quotas on the commercial fishery and creel limits on anglers.

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Effects of Intensified Fishing, Species Changes, and Spring Water Temperatures on Yellow Perch, *Perca flavescens*, in Saginaw Bay[1]

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ESHENRODER, R. L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34: 1830–1838.

A combination of intensified effort and size limit removal in the mid-1960s resulted in exceptional landings of yellow perch, *Perca flavescens*, from Saginaw Bay. Though gillnet effort increased from insignificance to account for more than half of the annual catch, gillnet catch per unit of effort (CPE) did not decline during the period of intensified fishing (1964–71) despite severe depletion on some grounds. Trapnet landings and CPE peaked in 1966, when the size limit was removed, but by the early 1970s both statistics were only one-third of the 1966 peaks. A fishing-up sequence began in outer Saginaw Bay and the stocks there were depleted. The fishery then shifted to the inner bay, where the stocks also declined, but to a lesser degree. With intensification of the fishery yellow perch growth rate increased, age-groups V–VII were no longer prominent in the catch and females became relatively scarce shortly after attaining vulnerability. The low recruitment of the late 1960s and early 1970s may have been related to the reduced brood stocks.

Within the past 35 yr those changes in the fish community which appeared to affect yellow perch most included loss of the walleye, *Stizostedion vitreum vitreum*, in the 1940s and proliferation of smelt, *Osmerus mordax*, and alewife, *Alosa pseudoharengus*, in the 1950s. However, these changes occurred well before the late 1960s, and were probably not involved in the recent yellow perch decline.

A comparison of the rate and regularity of the spring warming with the strengths of the strongest and weakest year-classes for the years 1957–75 suggested that spring temperature had an important role in reproductive success.

Key words: Percidae, *Perca*, yellow perch, exploitation, Saginaw Bay, Lake Huron, water temperature, fish community, population trends, history of fishery, Great Lakes

ESHENRODER, R. L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34: 1830–1838.

Un effort de pêche accru et l'enlèvement de la limite de taille au milieu des années 1960 résultèrent en des débarquements exceptionnels de perchaude, *Perca flavescens*, de la baie Saginaw. Bien que l'effort de pêche aux filets maillants ait augmenté de presque nul qu'il était pour capturer plus de la moitié de la prise annuelle, la prise par unité d'effort (PPE) des filets maillants ne diminua pas durant la période de pêche intensive (1964–71) en dépit de l'épuisement de certains lieux de pêche. Les débarquements et la PPE des filets-trappes atteignirent un sommet en 1966, quand la limite de taille disparut, mais au début des années 1970, ces deux statistiques n'étaient qu'un tiers des pics de 1966. Un processus de pêche en expansion commença dans la baie Saginaw extérieure, et les stocks y furent épuisés. La pêche se déplaça alors vers l'intérieur de la baie, où les stocks diminuèrent également, mais à un degré moindre. Avec l'intensification de la pêche, le rythme de croissance de la perchaude augmenta, les groupes d'âge V–VII cessèrent de prédominer dans la prise, et les femelles devinrent relativement rares peu de temps après être devenues vulnérables à la pêche. Il est possible que le faible recrutement de la fin des années 1960 et du début des années 1970 ait été lié à des stocks reproducteurs diminués.

Au cours des 35 dernières années, les changements dans la communauté de poissons qui semblent affecter le plus la perchaude incluent la perte du doré jaune, *Stizostedion vitreum vitreum*, durant les années 1940 et la prolifération de l'éperlan arc-en-ciel, *Osmerus mordax*, et du gaspareau, *Alosa pseudoharengus*, durant les années 1950. Cependant, ces changements se sont

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produits bien avant la fin des années 1960, et n'y étaient probablement pour rien dans le récent déclin de la perchaude.

Une comparaison de la vitesse et de la régularité du réchauffement printannier avec l'abondance des classes d'âge les plus fortes et les plus faibles durant les années 1957–75 suggère que la température printannière joue un rôle important dans le succès de la reproduction.

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THIS paper primarily examines the effects of intensified fishing and size limit removal on yellow perch, *Perca flavescens*, in Saginaw Bay during the 1960s. In addition a brief history of the yellow perch stocks from 1929 to 75, a review of those species changes in the fish community thought to have most affected yellow perch within the past 40 yr, a comparison of year-class strength with the spring warming and the results of a recent creel census are discussed.

With the demise of walleye, *Stizostedion vitreum vitreum*, in the 1940s, yellow perch became the most economically important component of the fish community in Saginaw Bay. For many years the yellow perch stocks supported extensive recreational and commercial fisheries. Beginning in the mid-1960s an improved market price stimulated an intensified commercial fishery for yellow perch in the bay, mainly by addition of gillnet fishermen to a fishery which had been dominated by trap netters. The statutory size limit was removed in 1966. By the late 1960s it was evident that the angler fishery had deteriorated, particularly in the outer bay, where the stocks had borne the initial thrust of the gillnet fishery.

Commercial catch sampling, initiated in 1960, made it possible to measure the effects of the intensified fishing on the stocks. Studies by Hile and Jobes (1941) and El-Zarka (1959) have also greatly contributed to an understanding and evaluation of the recent data.

Description of the Bay

Saginaw Bay is a shallow and productive extension of Lake Huron on the Michigan shore. Its physicochemical conditions are summarized in Table 1. Two large points of land and several islands reposing on a shoal divide the bay into inner and outer zones, which are approximately equal in area.

The inner bay is shallow, does not undergo permanent summer stratification, and contains extensive marshland. Its major tributary, the Saginaw River, drains a large industrial-urban complex and is the primary source of bay pollutants. Freedman (1974) summarized water quality data for the bay and there was some indication of improvement with declines in total dissolved solids in the 1970s and turbidity in the 1950s. However, the inner bay remains greatly enriched with industrial, domestic and agricultural waste and runoff. Despite this enrichment, frequent wind mixing of the water column normally maintains adequate levels of dissolved oxygen for fish.

Outer Saginaw Bay undergoes spring and fall overturns, and the hypolimnetic waters maintain high dissolved oxygen levels during summer stratification (Beeton et al. 1967). The outer bay shorelands are exposed to Lake Huron, and marshland is subsequently very scarce. Water quality in the outer bay is superior to that in the inner bay due to better mixing with Lake Huron.

Freedman (1974) discussed unpublished algal and zooplankton data from various surveys of Lake Huron and Schneider et al. (1969) described the benthos. Carr (1962) noted that 74 fish species were known from Saginaw Bay, and 38 species have been collected by trawl and gill net in recent Michigan Department of Natural Resources surveys.

Materials

Records of commercial landings for yellow perch in the bay date back to 1891 (Baldwin and Saalfeld 1962), but fishing effort and catch data were not collected on a systematic basis until 1929. Fishing effort and catch per unit of effort as used in this paper conform to Hile (1962). The monthly catch summaries submitted by commercial fishermen in the 1960s were sorted by fishing ground to determine whether the effects of sequential fishing (Lawrie and Rahrer 1972) were being masked by the conventional catch statistics.

Age and growth data from two papers are important in establishing the growth history of the stocks. The earliest account (Hile and Jobes 1941) was based on yellow perch collected from experimental pound nets in 1929–30. The second (El-Zarka 1959) dealt with samples collected from commercial trap nets during 1949–55.

Routine sampling of the trapnet fishery began in 1960 and has continued to the present. The early sampling (1960–65) was done by personnel from the United States Fish and Wildlife Service, Sandusky, Ohio. All fish were aged by personnel from the State of Michigan, Alpena Great Lakes Fisheries Station, who continued the collecting after 1965. Stock assessment with bottom trawls was initiated in 1970 by the State of Michigan, and today provides the basis for management. Details of the trawl assessment are given in Lake Huron Lake Committee Reports (1971–75) to the Great Lakes Fishery Commission.

History of the Fishery

Fishery gear and regulation — Beginning in 1929, when fishing effort was first recorded, and continuing

TABLE 1. Summary of physicochemical data for Saginaw Bay.

Item	Value	Source
Climate		
type	maritime	NOAA, Flint, Mich.
latitude (N)	43°50′	
average max. temp. (C)		
July	28.6	
January	0.1	
annual precipitation (cm)	76.6	
growing season (days)	218	
Drainage basin		
area (km²)	21,000	Freedman (1974)
human population (millions)		Anon. (1975a)
1940	0.6	
1970	1.2	
Effluent streams		
mean discharge (m³/s)		
8 largest rivers	115	Freedman (1974)
Saginaw River	96	Beeton et al. (1967)
Morphometry		Beeton et al. (1967)
length (km)	82	
width at mouth (km)	42	
total area (km²)	2,960	
mean depth (m)		
inner bay	4.6	
outer bay	15.6	
maximum depth (m)		
inner bay	14.0	
outer bay	40.5	
volume (km³)	27	
flushing rate (days)	186	
shoreline		
length (km)	265.5	Anon. (1975b)
development factor	1.38	
Chemistry		
specific conductance (μmhos)		Beeton et al. (1967)
inner bay	469	
outer bay	253	
Saginaw River mouth	800	
Lake Huron proper	174	Allen (1964)
alkalinity (ppm $CaCO_3$)		Beeton et al. (1967)
inner bay	110–125	
outer bay	90–110	
pH		Beeton et al. (1967)
June	7.8–8.1	
July	8.4	
total dissolved solids (mg/ℓ)		Bay City Water Plant
inner bay 1965	287	
1970	230	
1975	204	
turbidity (ppm)		Bay City Water Plant
inner bay 1930s	11.2	
1940s	20.7	
1950s	12.8	

through 1963 the trap net was the primary gear employed in the fishery. During these years trapnet fishermen accounted on the average for 80% of the yield. The remaining yield was divided between five other types of gear, of which the gill net was most prominent.

The period of intensified gillnet fishing began in 1964 with an influx of gillnet fishermen into outer bay ports. In this year gillnet effort (Fig. 1) was four times the 1929–63 mean. Gillnet effort declined after 1965, but still accounted for approximately one-half of the yellow perch catch until 1972. In 1972

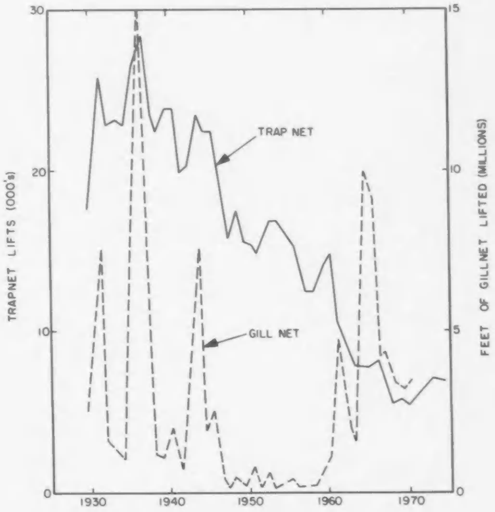

FIG. 1. Saginaw Bay fishing effort, 1929–74.

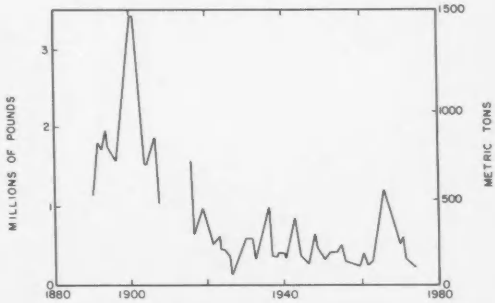

FIG. 2. Commercial landings of yellow perch from Saginaw Bay, 1891–1975.

the gillnet fishery was closed by regulation as a protective measure, and the trap net again became the predominant gear in the fishery.

Various size limits have been in effect during the yellow perch fishery. A minimum legal size of 22.9 cm (9 in.) governed the early (1908–36) fishery. In 1937 the limit was reduced to 21.6 cm (8½ in.) and this restriction was in force until 1965, when gillnet fishermen obtained a court injunction against its enforcement. In 1966, the size limit was removed for the entire fishery, and this condition had not changed through 1975.

Landings — The lengthy record (Fig. 2) of annual landings from the yellow perch fishery can be divided into three time periods. An early period, 1891–1916, of high landings was identified by both Hile and Jobes (1941) and El-Zarka (1959). Landings in this period averaged 545 t (1.2 million lb) and ranged between 450 and 1600 t (1.0 and 3.5 million lb). A second period of generally low landings continued until 1963. During these years (1917–63), annual landings averaged only 210 t (465,000 lb). In the third and most recent period, an abrupt increase in landings was succeeded by a gradual and persistent decline. Beginning in 1964 landings increased for 3 yr and in 1966 reached 545 t (1.2 million lb), the highest landings reported since 1916. Although yield remained exceptional just after 1966, the effect of the decline was substantial by the early 1970s. In 1974 yellow perch landings amounted to only 104 t (230,000 lb).

Fishing effort and catch per unit effort — The trend of trapnet fishing effort over the 45-yr period of record collection shows a number of sharp declines separating several periods of nearly constant effort (Fig. 1). In the years 1929–45 trapnet effort remained relatively high. Effort fell immediately after 1945, but tended to stabilize thereafter at 50–60% of the 1929–45 mean. After 1956 effort declined again, and since 1962 it has remained nearly stable at 20–25% of the 1929–45 mean.

The decreases in trapnet fishing effort reported after 1945 were not related to changes in the yield of yellow perch; trapnet landings did not change greatly during 1917–65. The trapnet fishery is a mixed-species fishery, and the near disappearance of other species, particularly the walleye (Hile and Buettner 1959), was responsible for the lower levels of trapnet effort.

The record of trapnet catch per unit of effort (CPE) has varied considerably from year to year, but until the 21.6 cm size limit was rescinded in 1966 no major trends were evident in the data. Fishing without a size restriction, the trapnet fishery in 1966 reported a record CPE — five times as great as the 1929–65 mean. A strong trend of declining CPE followed removal of the size limit. Catch per unit of effort in 1974 was one-third of the 1966 record.

Effects of Intensified Fishing on the Stocks from 1965 to 1974

Growth — Growth of yellow perch improved considerably after size limit removal in 1966. Males at the end of their fourth year averaged 16.3 cm in 1960–64 and 20.1 cm by 1968–71 (Table 2). Similar increases were evident for females and for other age-groups. Growth in 1960–64 was nearly identical to that reported by El-Zarka for 1949–55 (Table 2), and apparently had been relatively slow but stable for some time. The 1949–55 study was stimulated by complaints of fishermen that yellow perch were abundant in trapnet lifts, but few fish were of legal size; therefore, the slower growth rate probably persisted for over two decades. The rapidity and timing of the change in growth during the 1960s strongly suggest that increase in growth rate was related to intensification of fishing effort and size limit removal.

TABLE 2. Back-calculated total lengths (cm) at end of year for yellow perch from Saginaw Bay for various periods.

Period	Year of life							Sample size
	1	2	3	4	5	6	7	
				Males				
1929–30[a]	7.6	13.5	19.6	23.6	26.9	29.2	32.5	203
1949–55[b]	6.6	10.7	14.2	17.0	19.3	21.6	23.6	2,096
1960–64	6.9	11.9	14.7	16.3	18.8	20.3	22.1	126
1968–71	9.1	14.7	18.0	20.1	22.1	23.6	25.1	159
				Females				
1929–30[a]	7.6	13.5	20.6	24.4	27.2	29.2	30.7	600
1949–55[b]	6.9	10.9	15.0	19.1	22.4	25.6	28.2	1,305
1960–64	7.4	13.0	16.3	19.1	20.8	23.1		151
1968–70	8.9	15.5	19.8	22.9	25.4			37

[a]Data from Hile and Jobes (1941).
[b]Data from El-Zarka (1959).

TABLE 3. Percentages of yellow perch in various ages collected from Saginaw Bay commercial trap nets in the fall, 1960–74.

Year collected	Sample size	Age in annuli							
		I	II	III	IV	V	VI	VII	VIII
1960[a]	100		1	5	26	*31*	29	8	
1961	100		1	13	13	*24*	*24*	20	5
1962	100		4	*52*	22	12	6	2	2
1963	—		—	—	—	—	—	—	—
1964	147			2	31	*56*	7	4	
1965	100			21	24	*29*	21	5	
1966	200		6	5	*50*	16	18	5	
1967	100		23	20	16	*30*	11		
1968	100		6	*81*	4	7	2		
1969	100		17	24	*56*	3			
1970	100		11	21	15	*50*	1	1	1
1971	105	2	*90*	7			1		
1972	126	5	41	*51*	3				
1973	268		23	*68*	9				
1974	141		10	*68*	20	2			

[a]The 1960–65 collections made by U.S.B.S.F.W., Sandusky, Ohio.

El-Zarka (1959) indicated that yellow perch growth in the bay was density dependent during 1929–55. He noted that growth in 1949–55 was much slower than that reported by Hile and Jobes (1941) for 1929–30 (Table 2), and he estimated the stock had increased sevenfold over the same years. Yellow perch were considered to be at an extremely low level of abundance in the 1920s, and Hile and Jobes (1941) reasoned that the stock had been overfished. The association of faster growth with lower levels of stock is therefore strong for yellow perch in the bay, and El-Zarka's (1959) conclusions regarding density dependent growth are supported by the data for the 1960s and 1970s. Growth in this stock has fluctuated greatly over a 40-yr period, and the reported changes have all been associated with changes in the fishery that reflected stock abundance.

Age composition — After intensification of the fishery in the mid-1960s, the age composition shifted towards younger fish. Yellow perch at ages V–VIII were well represented in trapnet lifts from the early 1960s, but by 1968 fish at these ages were becoming scarce (Table 3). Except for the appearance of the very strong 1965 year-class in 1970, these older age-groups remained poorly represented to 1974. The near disappearance of older yellow perch from samples collected after 1967 was undoubtedly related to higher fishing mortality associated with the expanded gillnet fishery and the rescission of the size limit. Yield in the mid-1960s was evidently exceeding recruitment as trapnet CPE and mean age were declining while growth was increasing.

Spawning stock — Spawners, especially females were much reduced in abundance after fishing was intensified (R. Eshenroder unpublished data) so that the generally low reproduction after 1965 was presumably related at least in part to the reduced brood stocks. Trapnet CPE by 1974 was but one-third of that reported in 1966, when trapnet fishing was first conducted without a size limit. The actual reduction in stocks must have been greater than two-thirds, for the fishery was advantaged with faster growth in the more recent years.

The effects of the reduced stocks on spawning were compounded by faster growth, which enabled the fishery to exploit females before their first spawning. One-half of the females from the stronger and well sampled 1969 year-class first spawned in 1971, and the remaining half first spawned in 1972 (R. Eshenroder unpublished data). The later maturing females became vulnerable before their first spawning. Samples from the landed trapnet catch in the fall of 1971 were 86% females from the 1969 year-class. In contrast, nearly all of the landed catch under conditions of slow growth and a 21.6 cm size limit were of mature fish. Consequently, the reduction in spawning potential was greater than is implied in the decline of trap net CPE.

Female yellow perch, growing faster than males, were recruited to the trapnet fishery earlier, and in turn were eliminated sooner from the stock. Trawl samples (October) of the 1969 year-class at age III were only 11% female (R. Eshenroder unpublished data). On the basis of the shift in sex ratio, it was calculated that mortality of females from the 1969 year-class was not less than 90% at age III. Likewise the preceeding strong year-class, the 1965, was dominated by males after 2 yr of fishing. At age IV, trapnet samples of the 1965 year-class were only 16% female, and at age V, when one-half of the sample was yet of this year-class, no females were found. Before 1966, older females outnumbered males in samples from the stronger 1959 year-class after 3 yr of fishing. Female depletion then is a recent characteristic of the stock, and presumably had a negative effect on reproduction.

Distribution and abundance — The effects of intensified fishing on the abundance of yellow perch varied considerably between inner and outer Saginaw Bay. Throughout the period of intensified fishing the trapnet fishery operated mainly in the inner bay and fished the same grounds. Trapnet CPE declined markedly after 1966, but during 1967–71 gear competition from gill nets may have affected trapnet CPE in the inner bay. Therefore a comparison of trapnet CPE in 1966 with CPE reported after 1971 would eliminate this potential bias. Trapnet CPE decreased by two-third between 1966 and 1974, and this reduction reflects the decline in abundance of marketable yellow perch in the inner bay following the intensified fishing.

Intensified gillnet fishing in the outer bay during 1964–66 resulted in the collapse of these stocks, but the severity of the change was not reflected in the record of CPE. Initially the gillnet fishery operated on the northerly edge of the outer bay near the ports of Oscoda and East Tawas, but then fished progressively towards and into the inner bay. Gillnet fishermen maintained a rather consistent CPE by shifting to new areas, and accordingly the conventional catch statistics did not reveal the effect of the gillnet fishery on the outer bay stocks.

A sequetial fishing process (Lawrie and Rahrer 1972) was evident in gillnet landings from the outer bay during 1964–67. The initial thrust of the gillnet fishery was along the western shore of the outer bay. Gillnet landings amounted to only 33 t in 1963, averaged 163 t for the next three years and then fell to 12 t in 1967 and remained low thereafter. The gillnet fishery abandoned the western shore in 1967 even though it continued to operate out of outer bay ports while fishing the inner bay. If yellow perch were still abundant along the western shore after 1967, gillnet fishermen would not have made longer runs (an additional 2–3 h) to fish the inner bay, where the trapnet fishery operated. Division of the catch into distinct fishing grounds therefore suggests that depletion occurred in the outer bay after 3 yr of greatly expanded gillnet fishing.

Effects of Species Changes Since the 1940s

Species changes, particularly of salmonid fishes, within the fish fauna of Saginaw Bay have largely paralled the changes in Lake Huron proper as outlined by Smith (1972) and Berst and Spangler (1972). Lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, and lake herring, *C. artedi*, were all much reduced by the late 1940s, and chubs, *Coregonus* sp., declined in the early 1960s. These species were primarily associated with the deeper waters of the outer bay.

The native salmonid fish fauna in Lake Huron were replaced by rainbow smelt, *Osmerus mordax*, and alewife, *Alosa pseudoharengus* — exotic fish, which unlike the salmonids are abundant in inner Saginaw Bay over much of the summer (Carr 1962). In addition to the severe reduction of salmonid fishes, the walleye, which had been the dominant predator in the bay and the mainstay of the fishery, declined into insignificance in the 1940s. Together the loss of the walleye and the proliferation of smelt and alewife appear to be the changes in the fish community having the greatest effect on the yellow perch stocks.

Unfortunately, there are few data on the trend in abundance for either smelt or alewife in Lake Huron; neither species was fished even moderately in the bay. Smelt and alewives were both well established during the period when yellow perch were slow growing and very abundant. Smelt were first recorded in the bay in 1930 (Creaser 1932), and in the ensuing decade they became very abundant. The great smelt mortality of 1941–43 started in the bay area (Van Oosten 1947) and decimated this stock. Recovery was well under way by the late 1940s, and the greatest abundance may well have been attained by the early 1950s. Alewives were first recorded from Lake Huron in 1933 (Smith 1970), and were extremely abundant in the bay by 1956 (Carr 1962). Consequently, if either species had been inhibiting yellow perch recruitment, the effect should have been evident before the late 1960s, when recruitment did decline. Apparently therefore, neither smelt nor alewives restrained yellow perch recruitment when yellow perch were abundant.

Although it cannot be substantiated, the relationship between stock and recruitment may have been such that yellow perch reproduction was suppressed by either smelt or alewives under conditions of the smaller spawning stock. Yellow perch and alewives are in close association in the bay. Alewives are shoaling and very abundant during the spring shortly after yellow perch have spawned, and competition for food, if not predation, between adult alewives and yellow perch fry seems likely.

Of the major fish species now depleted in the bay the walleye was probably of closest association with yellow perch. Hile (1954) reported annual landings averaging 680 t in 1932–43, the last years of significant yield. The period of growth stagnation documented by El-Zarka may well have been influenced by the decline of the predatory walleye. Smith (1972) suggested that the absence of a predator, particularly lake trout, facilitated the ascendency of alewives in Lakes Michigan and Huron. The loss of the walleye could have had a similar effect in Saginaw Bay if walleyes were restraining yellow perch abundance before the 1940s. The period of slow growth and high abundance in the yellow perch stocks probably did not occur until after the walleye collapse, and therefore these events may be related.

Year-Class Strength and the Spring Warming during 1957–75

A qualitative comparison of the rate and regularity of the spring warming in Saginaw Bay with the exceptionally weak and strong year-classes suggests that spring temperature had an important bearing on reproductive success. Hartman (1972) suggested that spring temperature was an important factor in determining year-class strength for both walleyes and yellow perch in Lake Erie. Both species spawned strong year-classes in 1959, 1962, 1965, and 1970, and the first three of these were also exceptional in Saginaw Bay — a striking similarity. The pattern of yellow perch class strength in Thunder Bay, Lake Huron, was found to be similar to that of yellow perch in Saginaw Bay (R. Eshenroder unpublished data) with strong 1965 and 1969 year-classes in both areas. Likewise, walleyes from the Cheboygan River area of northern Lake Huron produced strong year-classes in 1965, 1969, 1972, and 1975, and this sequence with the exception of 1972 was identical with that of yellow perch in Saginaw Bay. Together these similarities in class strength suggest a common factor operating over a rather wide geographical area that markedly favored the development of strong yellow perch and walleye year-classes in Lakes Huron and Erie. The geographical separation between these stocks suggests a meteorological factor, and temperature during the reproductive phase of the life cycle as outlined by Hartman (1972) is conceptually appealing as a causative factor.

Daily water temperature readings taken at the Pinconning water plant, on the west shore of the inner bay, were used in determining the rate of the spring warming for the years 1957–75. As no observations were available on the actual timing of perch spawning each year, the warming period was taken to begin when a temperature of 10°C was first recorded. From this point slopes were calculated for multiples of 10-day periods. A comparison of these slopes with the known pattern of year-class strength indicated that the strongest relationship was obtained with a 30 day base period. This relationship was again improved by dividing the slopes by their standard errors

(*T*-statistic). In this manner deviations in the trend of warming were incorporated into the analysis.

A rigorous statistical analysis between the *T*-statistics and class strengths during 1957–75 cannot be developed. The commercial age composition data (Table 3) require adjustment to compensate for the changes in age at recruitment, and a reasonable method is lacking. The early scale collections contain few legal-sized fish, and therefore it would be very tenuous to project commercial CPE onto an age distribution of legal-sized fish. Furthermore, the change in size limit further separates the CPE data into two distinct trends, and these data are not readily reconciled. Consequently, a qualitative approach contrasting the *T*-statistics with those year-classes known to be exceptionally weak or strong is offered. The *T*-statistics for 1957–75 with notations (+ −) for the strongest and weakest year-classes of yellow perch were:

Year	*T*-Statistic	Notation
1957	−0.57	−
1958	8.30	
1959	14.41	+
1960	5.16	
1961	5.27	
1962	7.79	+
1963	4.83	−
1964	5.27	
1965	6.11	+
1966	2.49	
1967	2.61	
1968	1.30	−
1969	4.19	+
1970	4.04	
1971	9.09	
1972	19.41	
1973	0.38	
1974	2.45	
1975	29.58	+

The lowest *T*-statistic values occurred for years when warming was slow and/or irregular, whereas the higher values indicate a more consistent and faster warming. The *T*-statistic was lowest in 1957, 1968, and 1973, and two of the three weakest year-classes of record developed in those years (1957 and 1968). The major inconsistency between low T-statistic values and weak year-classes was with the 1963 year-class, which though weak was associated with a *T*-statistic of moderate value.

The relation between high *T*-statistics and strong year-classes was also somewhat inconsistent. Here the problem is the apparent lack of strong year-classes in 1958 and 1971–72, when *T*-statistic values were high. In fact the 1972 value was the highest of the series at that time. Interestingly, Cheboygan River walleyes and yellow perch in Thunder Bay produced strong year-classes in 1972, and it is here where the synchrony in year-class strength between these stocks failed. The higher *T*-statistic values in the years 1959, 1962, 1965, and 1975, when four of the five strongest yellow perch year-classes were spawned in Saginaw Bay, do suggest an important role for temperature in year-class formation. Busch et al. (1975) reported storm damage to walleye eggs in Lake Erie during 1969, and it seems likely that, despite favorable temperature conditions, a severe storm during incubation or hatching may have resulted in low survival. Accordingly, it may well be unwarranted to expect a perfect relationship between the spring warming and year-class strength.

Consideration must also be given to the reduction in adult stocks after the removal of the size limit in 1966. With the fishing-up of the older age-groups and growth acceleration, a dense stock of old spawners was replaced by fewer and younger fish from which some females now experienced exploitation before reaching maturity. Marked irregularity in year-class strength followed reduction of the walleye brood stock in Lake Erie (Busch et al. 1975), and the same phenomenon appeared to be developing in the bay. Five successive years (1970–74) without a stronger year-class can be viewed as reproductive weakness. The reduced brood stock may render reproduction more sensitive to environmental conditions such as the spring warming.

Angling

Saginaw Bay's recreational fishery is much more difficult to quantify, particularly in the past, than is the commercial fishery. Angling in the outer Bay declined severely after the expansion of the gillnet fishery in the mid-1960s. A number of outer bay ports such as East Tawas had been noted for their recreational fisheries, especially in the spring when thousands of anglers (International Board of Inquiry 1943) gathered to fish the perch spawning run. After 1970, when the outer bay was closed to commercial fishing for yellow perch, angling improved but remained well below the rates of the 1950s.

A creel census of ice fishermen along the west shore of the inner bay in 1975–76 indicated that angler catch and success were related to differences in availability of age III yellow perch. Angler success declined from 11.8 yellow perch per angler day in 1975 to 5.0 yellow perch per angler day in 1976. In 1975 an estimated 61%

of the angler catch was of this age group, whereas in 1976 only 26% were age III. In both years the remaining catch was of older fish. These data suggest that the recreational fishery may be strongly dependent upon the recruiting year-class, which in 1976 was weaker than in 1975.

No bay-wide census of summer anglers or winter census of east shore anglers has yet been undertaken in the bay. The east shore ice fishery is similar in size to that which was surveyed on the west shore, and the ice-free fishery is thought to be larger than the ice fishery. The yield in the west shore ice fishery was therefore at most one-quarter of the annual angler catch. West shore ice fishermen creeled a total of 10.6 t of perch in 1975 and 3.9 t in 1976. A minimal estimate of the total angler catch in 1975 would be 42.8 t. In that same year the commercial fishery landed 122.0 t of yellow perch. Accordingly, the commercial fishery was probably greater than the recreational fishery in terms of yield.

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Percids in the Canadian Waters of Lake Huron[1,2]

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SPANGLER, G. R., N. R. PAYNE, AND G. K. WINTERTON. 1977. Percids in the Canadian waters of Lake Huron. J. Fish. Res. Board Can. 34: 1839–1848.

Percids have never dominated the commercial catch from Canadian waters of Lake Huron but coincident with declining salmonid production, they contributed about 17% of the commercial landings from 1940 to 1975. Walleye (*Stizostedion vitreum vitreum*) production declined gradually over the past century whereas yellow perch (*Perca flavescens*) production increased irregularly since 1910.

Walleye occur in relatively discrete stocks associated with rivers, inlets, and estuaries in the North Channel and Georgian Bay whereas southern Lake Huron stocks are seasonal residents of the southeastern rim of the main basin. Yellow perch are ubiquitous throughout the littoral waters of the lake. Growth rates of walleye are similar to those for more southerly populations in the Great Lakes and year-class strength is highly variable. Angling and commercial fishing contribute significantly to mortality rates in exploited stocks but deteriorating environmental conditions are probably more important to the persistence of walleye stocks in Lake Huron. At least one stock is presently threatened by industrial acidification of the watershed.

Key words: Percidae, Lake Huron, production, population biology, *Stizostedion*, *Perca*

SPANGLER, G. R., N. R. PAYNE, AND G. K. WINTERTON. 1977. Percids in the Canadian waters of Lake Huron. J. Fish. Res. Board Can. 34: 1839–1848.

Les percidés n'ont jamais été dominants dans les prises commerciales des eaux canadiennes du lac Huron, mais, en même temps que déclinait la production de salmonidés, ils contribuèrent environ 17% des débarquements commerciaux entre 1940 et 1975. La production de dorés jaunes (*Stizostedion vitreum vitreum*) diminua graduellement au cours du siècle dernier, alors que celle de la perchaude (*Perca flavescens*) augmente de façon irrégulière depuis 1910.

Le doré jaune se rencontre en stocks relativement distincts associés aux rivières, petites baies et estuaires dans le chenal nord et dans la baie Georgienne, alors que les stocks du lac Huron méridional sont des résidents saisonniers de la bordure sud-est du bassin principal. La perchaude est omniprésente dans les eaux littorales du lac. Le rythme de croissance du doré jaune est semblable à celui des populations plus méridionales des Grands lacs, et l'abondance des classes d'âge varie considérablement. La pêche commerciale et la pêche à la ligne contribuent de façon significative aux mortalités dans les stocks exploités, mais la détérioration des conditions du milieu est probablement un facteur plus important de la persistance des stocks de dorés jaunes dans le lac Huron. Au moins un stock est présentement menacé par l'acidification industrielle du bassin hydrographique.

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THE objectives of this paper are to examine the role of percids in the fisheries and aquatic community of the Canadian waters of Lake Huron. Following a brief description of the Lake Huron environment we describe the distribution of percids in the lake and the historical contribution of percids to the fishery. Discussion of biological attributes is confined to those stocks that have been studied because some aspect of their exploitation has become contentious. Results of these studies are given in theses and manuscript reports prepared by a succession of biologists working under the auspices of the Ontario Ministry of Natural Resources. Our presentation relies heavily on the reports on walleye investigations for the Mississagi (Payne 1964, 1965, 1966), Shawanaga (Zimmerman 1967), and Moon rivers (Winterton 1975).

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Lake Huron Environments

Physiography and meteorology — Lake Huron (Fig. 1), the fifth largest lake in the world, is 330 km long, 293 km wide, and occupies 32% of its 186,480-km² watershed. The lake is divided into the relatively discrete water masses of the North Channel, Georgian Bay, and Lake Huron proper.

Most of the Lake Huron basin lies within the Paleozoic rock formation; the extreme eastern and northern parts of Georgian Bay and parts of the North Channel are underlain by Precambrian Shield (Hough 1958; Pincus 1962). The northern and northeastern parts of the watershed are forested with broadleaf and coniferous species; the remainder is mainly farmland.

The Lake Huron area is influenced by all the major airstreams on the continent. The climate is in the Continental Cool Summer category with air temperatures averaging about 20°C in July, the warmest month, and −5°C in January, the coldest (Bryson and Hare 1974).

Human influence on the watershed — Much of the watershed is sparsely populated (less than 8 persons/km²), particularly on the Canadian side, where the population has increased from about 414,000 in 1900 to 946,000 in 1970 (Upper Lakes Reference Group 1976). The population is concentrated in the lower basin of Lake Huron proper and Georgian Bay. Of the shoreline of Lake Huron, 69% is in agricultural or forested land, 26% in residential and recreational, and 5% is industrial and commercial (Lee and Beaulieu 1971).

One of the most conspicuous physical alterations of the watershed has been the construction of over 300 dams on the Canadian tributaries to the lake (Anon. 1966). Though many of these dams have no known direct effect on the lake, there are direct influences on the fish community through blocking of migration routes and manipulation of water levels or flow volumes over spawning areas (Winterton 1975).

Thermoelectric generating stations are few along the Lake Huron shore at present. The Canadian waters of Lake Huron now receive significant waste heat input only from the 300-MW Douglas Point nuclear reactor, but a larger plant at the same site will soon become operational.

The main bodies of water in Lake Huron are of good quality but there are four inshore areas where municipal wastes are causing problems and two tributaries (St. Mary's River and Spanish River) where phenolic effluents from industry have caused degradation (Great Lakes Water Quality Board 1974). Atmospheric fallout from metal smelters has acidified many waters tributary to the North Channel and Georgian Bay (Beamish and Harvey 1972; Conroy et al. 1976). This acidification now extends to the northernmost waters of Georgian Bay (Loftus 1976).

Limnology — The limnological characteristics of the major water masses of Lake Huron were summarized by Berst and Spangler (1973).

Variations in surface temperature across the lake are indicated by the isotherms derived by Strong (1974) from satellite infrared imagery. The map for June 14, 1973 (Fig. 2) reveals temperatures ranging from 4 to 18°C over the Canadian portion of the lake. High, nearshore temperatures are common in the bays and estuaries of eastern Georgian Bay where summer surface temperatures approach 27°C (Winterton 1975).

Vertical thermal stratification is apparent after late June or early July and persists until late fall. Thermocline depths in August usually range from 15 to 38 m (Ayers et al. 1956). Internal seiches of considerable amplitude (20–40 m) are common (Emery 1970) and may result in thermocline waters upwell-

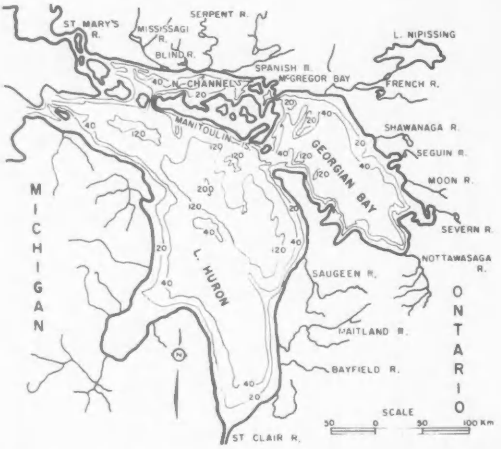

FIG. 1. Major water masses and tributaries of Lake Huron (depth contours in meters).

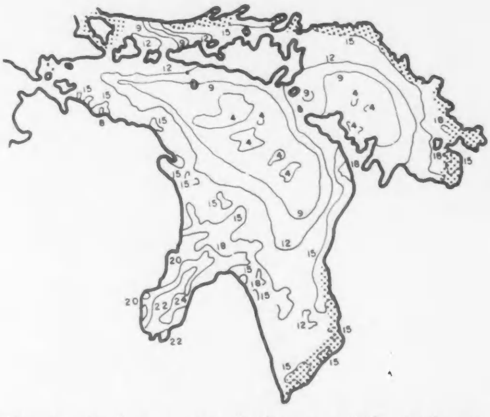

FIG. 2. Surface water isotherms (°C) (redrawn from Strong 1974) and distribution of walleye (stippled areas) in Canadian waters of Lake Huron.

ing at the surface at nearshore locations in Georgian Bay and the main basin (Strong 1974). Observations in southern Georgian Bay between August 22, 1975 and September 2, 1975 showed the 13°C isotherm rising from 37 m to 5 m (N. R. Payne unpublished data).

Although there is a concensus that the major water masses of the lake are oligotrophic, some inshore areas are becoming mesotrophic (Dobson et al 1974; Vollenweider et al. 1974).

Distribution of Percids

Eight species of percids occur in Lake Huron (excluding tributary streams): yellow perch, *Perca flavescens*; walleye, *Stizostedion vitreum vitreum*; sauger, *S. canadense*; Iowa darter, *Etheostoma exile*; johnny darter, *E. nigrum*; logperch, *Percina caprodes*; channel darter, *P. copelandi*; and the blackside darter, *P. maculata*. Two of these, sauger and channel darter, are common only in U.S. waters whereas the logperch, johnny darter, and yellow perch are common throughout inshore waters of the lake (Hubbs and Lagler 1958; Scott and Crossman 1973). Little is known about the distributions of the other darters because of their small size and unknown importance to man.

Walleye are confined principally to southern Lake Huron, eastern and northern Georgian Bay, and the northern waters of the North Channel (Fig. 2). They are fish of moderately shallow water (to 15 m) and tend to occur in the warmest waters of Lake Huron.

Documented cases of shoal spawning by walleye in Lake Huron are few but some spawning occurs along the southeastern shore of the main basin and spawning walleye have been observed in the channels between islands in McGregor Bay, an inlet of northern Georgian Bay (Zimmerman 1967). Walleye in ripe condition have also been observed along the shore of the North Channel between the mouths of the Mississagi and Blind rivers.

The yellow perch is ubiquitous throughout the inshore waters of the lake, although it is much more common in some areas than in others. In Georgian Bay, Craigie (1971) found yellow perch concentrations in the extreme north but they were most abundant in the warmer and shallower waters of the southern and eastern shores. In the North Channel, a limited survey found yellow perch in most inshore areas in midsummer with greater concentrations in the eastern end of the channel than in the west (Collins 1964). Yellow perch attained their greatest abundance in Canadian waters of the lake at the south end of the main basin which is the warmest part of the lake and also the portion having the greatest area inside the 18-m contour.

Percid Fisheries

Commercial exploitation of Lake Huron fish stocks by Canadians began in the 1830s. Initially, lake trout, whitefish, and ciscoes were the main species taken, but walleye and, later, yellow perch gradually assumed importance and remain significant constituents of the catch. The principal fisheries for these species are now located in the southern half of the main basin but walleye and, to a lesser extent, perch are also taken along the eastern shore of Georgian Bay and at several scattered points along the North Channel.

In spite of its general popularity among Ontario fishermen (Cox and Straight, circa 1976), angling for walleye in Lake Huron is generally confined to the eastern and northern shores of Georgian Bay, where islands or headlands offer protection from heavy seas. The highest concentration of walleye anglers in Lake Huron is found in the Port Severn–Midland area of southeastern Georgian Bay. Important walleye sport fisheries also occur in the channels and estuaries of the St. Mary's Mississagi, French, Moon, and Nottawasaga rivers. Perch are the favorite species of many pier fishermen and are caught by anglers in virtually all of the inshore areas of Lake Huron where angling occurs.

Yield — The percentage of percids in the commercial catch of all species ranged from 7 to 17 from 1900 to 1975. This percentage has been highest since 1940 as a result of declining production of salmonids, for the combined catch of walleye and yellow perch has increased only slightly (Fig. 3).

Walleye production declined from 369 t in the 1900s to 57.7 t (5-yr average) during the first half of the 1970s; yellow perch production increased from 39.3 t (10–yr average) in the 1900s to 199.4 t in the 1960s; sauger have never been a significant component of the Canadian catch. The production of all species is characterized by an increasing trend from the mid-1860s until the turn of the century, followed by relatively stable production until the mid-1930s and rapidly declining production until 1947. The subsequent peaks in production in 1953 and 1961 were due to outstanding catches of coregonines (Berst and Spangler 1973).

Walleye production during the last century appears to have been somewhat irregular until about 1895. Then came a slow, steady decline until the mid-1940s, followed by a slight recovery in 1948 and an irregularly decreasing catch until 1969. The abrupt decline in 1970 was due to the temporary closure of the fishery in southern Lake Huron because of high levels of methylmercury in the edible flesh of walleye. Throughout this century, walleye have commanded a premium price on the market, so that the lows in production are unrelated to lowering of demand. We

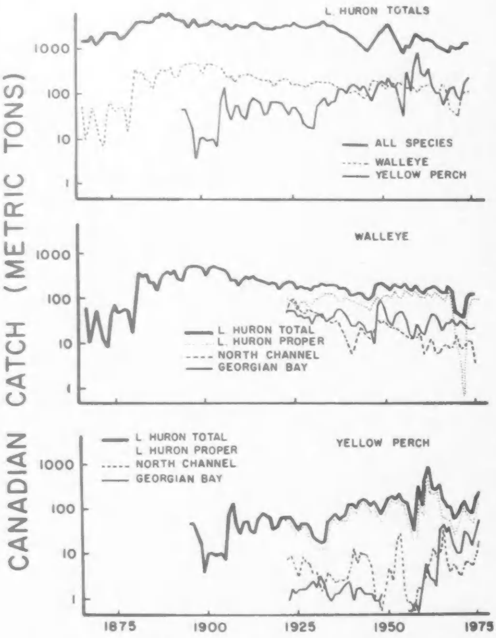

FIG. 3. Production of walleye and yellow perch by basin (since 1923) and total production of all commercial species from Canadian waters of Lake Huron. Data for 1867–1968 are from Baldwin and Saalfeld (1962 + Supplement). Landings for 1969–75 are from Ontario Ministry of Natural Resources, Toronto, Ontario.

doubt that the increase in angling catch has compensated for the decrease in commercial production of walleye during this century.

Yellow perch production has been markedly irregular over the entire history of the fishery; however, there has been an increase in yield since the early 1900s with production during the 1960s averaging almost 440 t. Much of the variation in the annual catches of yellow perch probably resulted from the generally low market value of this species; fishermen tended to fish for perch only when other species were exceptionally scarce.

The apparently stable production of walleye for all areas together contrasts with the strongly fluctuating yields from each of the basins. For example, Georgian Bay catches increased almost tenfold from 1947 to 1949 while North Channel and main basin yields increased less than 50%. There is little synchrony in yield between the fisheries in the three basins.

Yellow perch production depended far more upon the main basin than upon Georgian Bay or the North Channel. Georgian Bay catches were almost insignificant until the mid-1960s, when production rose abruptly to 35.4 t and averaged 31.3 t, over the next decade. Unlike the walleye statistics, perch production figures have tended to be approximately synchronous over the three basins. From 1922, when production was first recorded separately for each basin, until the mid-1940s, North Channel production peaks and lows lagged 1 yr behind the corresponding peaks and lows in Georgian Bay.

Population Biology of Walleye

Several discrete stocks of walleye are identifiable in the Canadian waters of Lake Huron (Payne 1965; Zimmerman 1967; Ferguson and Derksen 1971; Winterton 1975). In the North Channel, the St. Mary's, Mississagi, Serpent, and Spanish rivers and estuaries harbor walleye populations as does McGregor Bay at the east end. In Georgian Bay there are walleye associated with the French, Shawanaga, Seguin, Moon, Severn, and Nottawasaga rivers. Shoal spawning stocks have been identified in the Groundhog Island area (off the Shawanaga River) and at the Bayfield–Nares Inlet area approximately 10 km farther north. Little is known about the southern, main basin stocks some of which spawn in the Thames River (tributary to Lake St. Clair) returning soon afterwards to the St. Clair River and southern Lake Huron. Ferguson and Derksen (1971) suggested that the southern Lake Huron population consisted of at least two spawning stocks since fish tagged in Lake Huron were subsequently recovered in the Thames River and even farther downstream in the Detroit River and western Lake Erie.

Range and movement — In the North Channel, the Mississagi walleye spawn below dams in the Mississagi and Blind rivers at distances of 29 km and 250 m, respectively, from the river mouths. Dispersal after spawning is quite rapid with rates sometimes exceeding 1 km/day. During May and in late summer and fall the walleye are mainly confined to the river mouths and waters of the North Channel within 10 km and tend to concentrate in a wedge-shaped territory inshore of the 10-m depth contour. Throughout the summer a small concentration of fish remains in the channel in association with the Blind river outfall and substantial numbers of walleye inhabit the Mississagi River. Virtually no movement occurs across the North Channel to Manitoulin Island but a few tagged fish have been taken as far east as Serpent River.

In Georgian Bay, the Shawanaga stock disperses throughout the lower river during the summer; only during extremely hot summers do walleye move out into Shawanaga Bay. Zimmerman (1967) found that less than 10% of the fish tagged during the spawning period were recovered more than 5 km from the tagging location. Similarly, the stock spawning in the Groundhog Island area dispersed throughout the outer islands, generally traveling less than 5 km although occasional "wanderers" traveled 50–80 km or more along the Georgian Bay shore.

The Moon River stock consistently utilizes either of two spawning sites 10.5 km apart. A few fish are known to have utilized the two sites in successive seasons thus suggesting a homing tendency which may not be strongly site-specific.

After spawning, older Moon River walleye apparently move to offshore island areas in Georgian Bay. Most of these fish move south to summer grounds approximately 35 km from the spawning site while some walleye move northward a similar distance. Younger walleye tend to remain among the islands near the mouth of the Moon River. During late fall and winter, there is a general movement toward the mouth of the river.

Growth — Walleye in the Mississagi, Shawanaga, and Moon rivers, and Groundhog Island areas exhibit exceptionally fast growth (Fig. 4) in spite of their location in northerly latitudes. The Mississagi fish (the slowest growing of the four stocks) attain a fork length of 25 cm in 2 yr and 50 cm in approximately 6 yr. The Moon, Shawanaga, and Groundhog stocks grow slightly faster but not so fast as walleye in Great Lakes waters farther south, namely, Lake Erie (Parsons 1972), the Bay of Quinte in Lake Ontario (Payne 1964), and Saginaw Bay (Hile 1954). Lake Huron walleye apparently grow more rapidly than walleye from many inland waters (Payne 1964).

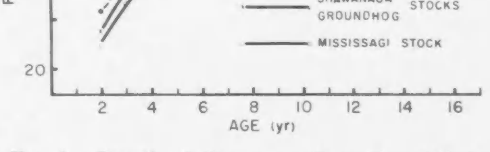

FIG. 4. Growth of Shawanaga–Groundhog, Mississagi, and Moon River walleye (mean lengths from spring trapnet samples). Data are from Payne (1965), Zimmerman (1967), and Winterton (1975).

The relation between length and weight of Mississagi and Moon river walleye, respectively, is described by the equation

$$\log_{10}W = 2.907 \log_{10}L - 4.772 \ (r = 0.997)$$
$$\log_{10}W = 3.456 \log_{10}L - 5.683 \ (r = 0.990)$$

where W is the weight in kilograms and L is the fork length in centimetres. The relatively high value of the slope for the Moon River stock is due to the presence of gravid fish in the sample. The Mississagi relationship was based on fish taken throughout the fishing season.

Diet — Little is known about the food habits of walleye in the Canadian waters of Lake Huron. Examination of stomachs of 251 Mississagi walleye collected from May to September, 1965 and ranging in length from 25 to 73 cm, revealed fish remains in all instances but two in which insects were found. Rainbow smelt (*Osmerus mordax*) the predominant food species in May, contributed 14.9% of the identifiable fish for the sampling period; they were absent in July and August and reappeared in stomachs in September. Alewives (*Alosa pseudoharengus*) were the dominant prey during August and September, constituting 80.4% of the identifiable fish remains. Yellow perch, important in the diet of walleye in other waters, were not observed in any of the stomachs examined although they were commonly captured in the same nets in which walleye were taken (Payne 1965).

Reproduction — Walleye in Lake Huron are older at maturity than those in the lower Great Lakes (Payne 1964; Regier et al. 1969; Parsons 1972). Some males mature as early as age III (approximately 10% in the Mississagi stock) but most are not mature until age IV or V. Females appear in the spawning runs as early as age IV (about 10% in Mississagi stock) and most are mature by age V.

Spawning dates for the Mississagi stock range from about April 20 to May 15, whereas the Shawanaga, Groundhog, and Moon River stocks spawn from mid-April to the end of May with peak activity usually in the first 2 wk of May.

Fecundity of the Moon River walleye is almost identical (Winterton 1975) to that of the Bay of Quinte stocks (Payne 1964). The relationship of

TABLE 1. Estimated numbers[a] of fish of ages III–VII in the Mississagi walleye population in the springs of 1965 and 1966 and between-year mortalities.

	Age				
	III	IV	V	VI	VII
1965	11375±3790	1944± 742	967±473	1448±818	
1966	8525±6058	5397±1121	746±443	381±221	713±466
% mortality between years	52.6	61.6	60.6	50.8	

[a] Adjusted Petersen estimates and confidence intervals computed by formulae in Ricker (1975, p. 78).

body weight in grams (W) to egg numbers (Y) is:

$$\log_e W = 1.193 + 1.375 \log_e Y \ (r = 0.969).$$

Population estimates and mortality rates of walleye — Petersen estimates for the Mississagi stock in 1965 and 1966 (Table 1) indicated a decline from 15,734 to 7,237 walleye over the year for age-classes III–VI. The higher mortalities, between ages IV and V and V and VI, probably reflect the efficiency of 114-m (stretched measure) gill nets for walleye of these ages.

Fishing mortality (Table 2), corrected for tag loss and incomplete reporting of tags, averaged 0.204 over ages III–VI with no trend apparent toward reduced vulnerability with increasing age. Natural mortality for the year beginning in the spring of 1965 was estimated as 30% of the stock of age III–VI walleye or a conditional natural mortality rate of 36%.

The few estimates available for the Shawanaga and Groundhog Island stocks (Table 3) indicate that these populations were not large during the mid-1960s. The apparent decline in abundance was reflected by a decreasing yield to the commercial fishery for the Groundhog Island stock and a declining catch per unit of angling effort for the Shawanaga stock.

Catch curve analysis of the Groundhog Island stock indicated a mean annual mortality rate of 60.2% for age-classes IV–IX from 1962 to 1967 (Table 4). During the same period, the Shawanaga stock endured an annual mortality rate averaging only 32.5%. The Groundhog Island samples contained very few fish older than age VII while the Shawanaga data included substantial numbers in all age-classes from IV to XIII.

Zimmerman (1967) attributed the apparent difference in mortality rates between these stocks to different levels of exploitation by the commercial and recreational fisheries. The Groundhog Island fish recruited to the commercial gill nets (114-mm stretched measure) at age IV. This gear remains maximally efficient for walleye until they grow beyond a fork length of 70 cm (Hamley and Regier 1973). The growth rate of the Groundhog Island stock (Fig. 4) allowed virtually no escapement from the gear until after age XII.

TABLE 2. Mortality rates for Mississagi walleye from 1965 to 1966. Notations follow Ricker (1975).

	Age				
	III	IV	V	VI	Mean
Fishing					
Angling	.192	.240	.178	.204	.204
Commercial	.027	.065	.060	.040	.048
Experimental	.014	.018	.015	.011	.014
Total (u)	.233	.323	.253	.255	.266
Annual expectation of death					
Total (A)	.526	.616	.606	.508	.564
Fishing (u)	.233	.323	.253	.255	.266
Natural (v)	.293	.293	.353	.253	.298
Instantaneous rates					
Total (Z)	.747	.957	.931	.709	.836
Fishing (F)	.331	.502	.389	.356	.394
Natural (M)	.416	.455	.542	.353	.442
Conditional rates					
Total (A)	.526	.616	.606	.508	.564
Fishing (m)	.282	.394	.322	.300	.324
Natural (n)	.340	.366	.418	.297	.355

Shawanaga walleye recruited to the angling fishery at age III. Despite this earlier entry into the fishery, the lower total mortality rate of this stock (and consequent persistence of older fish) suggests that the recreational fishery was having minimal impact upon the Shawanaga population.

The Moon River stock must be one of the largest walleye populations in Georgian Bay. Schnabel and Petersen estimates for the 1968 and 1969 spawning runs (Winterton 1975) were:

	1968	1969	1970	1971	1972
Schnabel	20,826	22,443			
Petersen	24,124	23,265	19,907	16,989	12,739

TABLE 3. Abundance of walleye in spring and summer (estimated by the Schnabel method) in the Shawanaga and Groundhog Island stocks, 1962–67 (Zimmerman 1967).

	Shawanaga	Groundhog Island
1962		
Spring	1531 (429)[a]	4021 (298)
Summer	1259 (141)	2320 (278)
1963		
Spring	1476 (859)	13669 (293)
Summer	—[b]	9469 (727)
1964		
Spring	1861 (1515)	951 (139)
Summer	—	4029 (334)
1965		
Spring	2921 (1208)	—
Summer	—	704 (199)
1966		
Spring	2005 (1164)	—
Summer	—	192 (100)
1967		
Spring	1002 (697)	—
Summer	—	738 (90)

[a] Numbers of fish tagged and recaptured.
[b] Sample too small to provide estimate.

Mortality rates for the 1957–65 year-classes averaged 34.9% from 1968 to 1972 (Table 5). Tag returns from the Moon River walleye indicated similar levels of exploitation by sport and commercial fisheries from 1969 to 1972. Anglers annually harvested 11–22% of the available stock and the commercial gear caught 12%. Total harvest ranged from 11,500 in 1969 to 4,000 in 1972 or, 24 and 32%, respectively, of the available walleye (Winterton 1975).

Year-class strength and variation — From 1955 to 1963 year-class strength varied more than 12-fold in the Mississagi stock and more than 15-fold in the Moon River stock (Fig. 5). The 1955 and 1959 year-classes were exceptionally strong. The Moon River produced a very large year-class in 1960 and then four weak year-classes in succession. The Shawanaga and Groundhog Island stocks produced large year-classes in 1955, 1959, and 1960.

The strong year-classes of walleye in 1955 and 1959 coincide with relatively strong year-classes of this species in the Bay of Quinte of Lake Ontario (Payne 1964). While weaker than many year-classes before 1955, the 1955 and 1959 year-classes were among the strongest to emerge from 1955 to 1961 in Lake Erie (Parsons 1970). The 1956–58, 1960, and 1961 year-classes were poor to moderate in all of these areas except that eastern Georgian Bay produced exceptionally large year-classes in 1959 and 1960.

Percid Responses to Abiotic Factors

Temperature is probably the most conspicuous factor influencing walleye in Lake Huron. There is a remarkable similarity between the discontinuous distribution of walleye and surface waters within the 15°C isotherm (see Fig. 2). This suggests that temperature may be one of the most important factors in determining the distribution of walleye in the lake.

The summer exodus of walleye from the Moon River islands area was attributed by Winterton (1975) to excessive water temperatures. Walleye catches were highest where deeper sets (8 m) were made at temperatures of 18.5–19.5°C. Winterton (1975) also suggested that migration routes of walleye along the Georgian Bay shore between the Moon River and the summer grounds may have been the result of a thermal impoundment by the colder offshore Georgian Bay water. This agrees with Ryder's (1968) conclusion that the deep, cold water between Nipigon Bay and Black Bay provided an ecological barrier to walleye movements in Lake Superior.

Temperature is probably one of the physical factors responsible for the absence of walleye in great numbers from the major water masses of Lake Huron. Very low temperatures continuing well into the summer may preclude successful spawning on shoals which would otherwise be satisfactory. Thermal instability during the sum-

TABLE 4. Total annual mortality estimates (percent) for Shawanaga and Groundhog Island walleye from age compositions of combined samples of spring and summer trapnet catches, 1962–67 (Zimmerman 1967).

	Age-class					
Stock	IV–V	V–VI	VI–VII	VII–VIII	VIII–IX	Mean
Shawanaga	35.5	41.0	33.6	32.3	20.2	32.5
Groundhog Island	76.1	69.0	61.5	48.0	46.2	60.2

TABLE 5. Mortality rates for year-classes of the Moon River spawning stock of walleye, 1968–72. Number of fish present in each year of capture by trap nets is based on the age structure of the spawning stock calculated by Petersen estimates (Winterton 1975). Symbols follow Ricker (1975).

	Year-class									
Year of capture	1957	1958	1959	1960	1961	1962	1963	1964	1965	Total to 1963
1968	357	499	2022	13134	1473	1199	3221			21905
1969	440	498	1905	7708	1084	1114	2345	1993		15094
1970	123	368	809	4585	1128	711	1103	1201	10837	8827
1971	72	126	485	3052	1131	844	1149	916	6805	6859
1972	25	88	200	1590	751	501	651	488	6524	3806
				Catch curve analysis						
Z	.7226	.4845	.5995	.5149	.1305	.2023	.3911	.4492	.2537	.4291
A	51.5	38.4	45.1	41.3	12.2	18.3	32.4	36.2	22.4	34.9
$\bar{Z} = 0.4165$										
$\bar{A} = 0.341$										

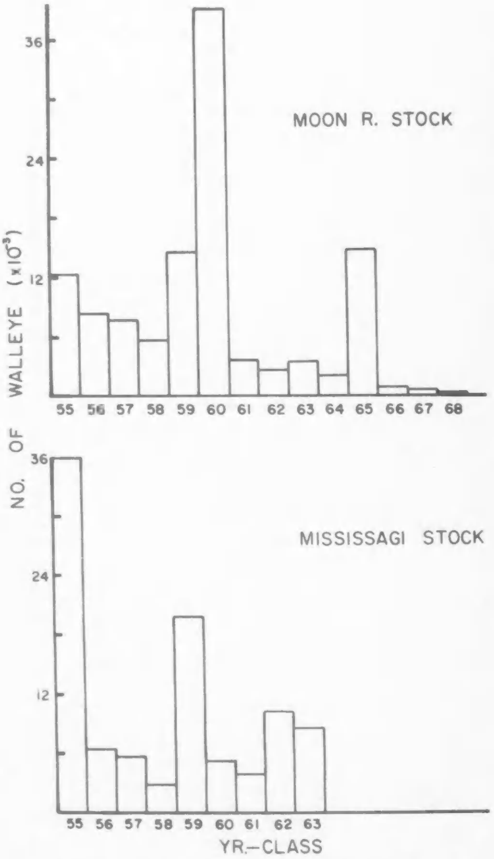

FIG. 5. Estimated year-class strengths of Mississagi walleye at age III (Payne 1965) and Moon River walleye at age V (Winterton 1975).

mer (due to internal seiches) may preclude walleye occupation of portions of the littoral zone not protected by offshore islands.

Yellow perch in Lake Huron commonly range down to the thermocline, going deepest in warm years and in fall during turnover. We agree with Wells' (1968) conclusion that temperature determines the depth to which perch will go.

Temperature also affects growth rates of yellow perch. In South Bay of Lake Huron, Coble (1966) found a strong relationship between growth of female perch and June–October temperatures at the 6-m contour. He concluded that these perch began to grow at water temperatures of 12.5–13.0°C.

Little is known about the general effects of water flow and water quality on percids in Lake Huron, but Winterton (1975) found that variation in year-class success of Moon River walleye was strongly correlated ($r = 0.92$ for 1959–68) with flow volumes during the spawning period. Low, stable flows did not appear to produce strong year-classes.

Deterioration of water quality in the Spanish River, downstream from the kraft mill at Espanola, Ontario, has been responsible for taste and odor problems in walleye caught near the mouth of the river (Anon. 1972). Although the abundance of walleye in that area is not known, the fishery has declined substantially.

The McGregor Bay stock is much less abundant now than during the 1950s and early 1960s and apparently consists of only a few very old fish. We suspect that acidification of the McGregor Bay watershed might be responsible for the recruitment failures in the walleye population since pH readings as low as 5.3 have been recorded there in mid-August (Loftus 1976).

Conclusions

A long-term trend of declining production of walleye is evident in the catch statistics of the past century but walleye stocks do not appear to be alarmingly low in any of the three basins of the lake. The increase in yellow perch yield from 1910 to 1975 was not necessarily due to changes in the basic productivity of the lake as the yield of all commercial species from Canadian waters declined irregularly from 1930 to 1975.

Growth rates of Lake Huron walleye are generally rapid and mortality rates are not obviously excessive but a few stocks exhibit markedly contracted age distributions. Annual spawning does not provide a constant level of recruitment and individual year-classes dominate the populations at irregular intervals.

Walleye populations in Lake Huron are so conspicuously dependent upon environmental conditions in tributaries and estuaries that loss of individual stocks or changes in water quality of these fluvial environments should be taken immediately as the bellwether of things to come for Lake Huron as a whole.

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Depreciation of the Warmwater Fish Community in the Bay of Quinte, Lake Ontario[1,2]

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HURLEY, D. A., AND W. J. CHRISTIE. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

The sequence of fish species shifts since the 1930s in the Bay of Quinte is interpreted in terms of climatic changes and the influences of man. Among the latter, eutrophication is judged most important. The marked decrease in large piscivores in both eastern Lake Ontario and the Bay of Quinte as a consequence of these changes resulted in instability, exemplified by the explosions in populations of alewife (*Alosa pseudoharengus*) and white perch (*Morone americana*). Nutrients are imported to the bay, from Lake Ontario by way of alewife. This source has increased in the 1970s with the further decline of piscivores, and it brought about a greater fish production in the bay. We conclude that the Bay of Quinte and Lake Ontario interact significantly and should be studied as a single system.

Because of its specialized feeding habits, the post-World War II rise of the walleye (*Stizostedion vitreum vitreum*) was related to events outside the Bay of Quinte, but its later decline was attributable to direct and indirect effects of eutrophication. Yellow perch (*Perca flavescens*), by contrast, were apparently not affected adversely by severe habitat changes induced by cultural eutrophication.

Key words: Percidae, community ecology, species shifts, eutrophication, habitat changes

HURLEY, D. A., AND W. J. CHRISTIE. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Nous interprétons la succession des espèces de poissons depuis les années 1930 dans la baie de Quinte en termes de changements climatiques et d'influences de l'homme. Parmi ces dernières, nous considérons l'eutrophisation comme la plus importance. Le déclin marqué des grands piscivores, tant dans le lac Ontario oriental que dans la baie de Quinte, comme conséquence de ces changements entraîna une instabilité qui se manifesta par l'explosion des populations de gaspareaux (*Alosa pseudoharengus*) et de bars-perches (*Morone americana*). La baie reçoit des éléments nutritifs du lac Ontario par voie du gaspareau. Cette source est devenue plus abondante pendant les années 1970 avec le déclin plus prononcé des piscivores, et il en est résulté une production de poisson accrue dans la baie. Nous concluons qu'il y a action réciproque entre la baie de Quinte et le lac Ontario, et que les deux devraient être étudiés comme système unique.

A cause des mœurs alimentaires spécialisées du doré jaune (*Stizostedion vitreum vitreum*), on a associé l'augmentation dans l'abondance de cette espèce après la Seconde guerre mondiale aux événements qui se sont produits en dehors de la baie de Quinte, mais son déclin subséquent est attribuable aux effets directs et indirects de l'eutrophisation. La perchaude (*Perca flavescens*), par contraste, ne semble pas avoir été adversement affectée par les profonds changements de l'habitat provoqués par l'eutrophisation culturale.

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As a contribution to PERCIS we present a case history of the Bay of Quinte based on long-term shifts in fish species composition and abundance determined from commercial catch statistics and from experimental fishing. However, this case history differs from those for more northern and ecologically "simpler" systems because natural changes in climatic features and man-induced changes in limnological characteristics occurred during the time that shifts in fish species composition were noted. We attempt to integrate the climatic and limnological changes with changes

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in fish species and abundance to form a plausible sequence. Much of this sequence, however, rests on interpretation of the case history data.

The fish community of the Bay of Quinte differs in two important respects from other North American communities containing percids. First, the southern location ensures that the percids share the habitat with centrarchids, esocids, percichthyids, cyprinids, and other families. Though percids have at times been very important in biomass terms, their dynamics cannot be viewed in isolation from the other members of the warmwater fish community. Secondly, the Bay of Quinte opens into Lake Ontario and events in open Lake Ontario have profoundly influenced the bay fish community.

Description of Bay

Physical — The Bay of Quinte lies in the northeast margin of Lake Ontario between the mainland and the Prince Edward County peninsula (Fig. 1). Morphometric data for the three sections that correspond to the areas of its Z-shape are given in Table 1. The bay becomes progressively wider and deeper from the upper to the lower end. The major centers of population are located in the upper bay.

Significant river inputs to the Bay of Quinte occur only in the upper bay between Trenton and Napanee (Fig. 1). Peak flow occurs in April and minimum flow in late summer. Only a few streams enter the bay on the Prince Edward County side. Demorestville Creek and Sawguin Creek drain lowland and extend through extensive marsh area.

The hydrologic turnover time in the bay between December and April is approximately one month. The annual turnover rate averages 5–7 times per year, and in the area above Glenora is 9–13 times per year. In the shallow upper bay, river inputs become completely mixed to all depths.

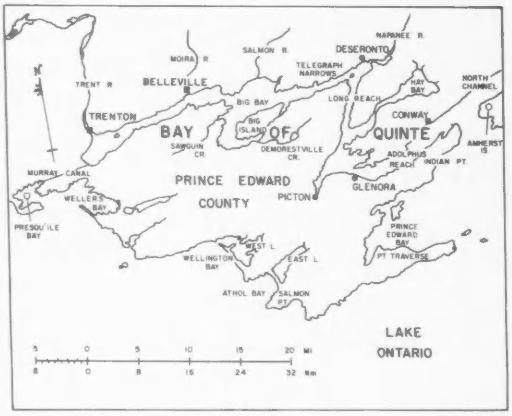

FIG. 1. Eastern Lake Ontario and the Bay of Quinte.

The bay joins Lake Ontario at either end of Amherst Island. The western passage is 3 km wide with a narrow benthic channel which deepens to 25 m. The eastern passage is also 3 km wide with a narrow outlet trench deepening to 33 m.

Fish habitat — Fish habitats in the bay range from shallow gravel bars, sandy inlets with macrophyte beds and cattail marshes to the steep-sided Adolphus Reach which thermally stratifies. Lower portions of the Trent, Moira, Salmon, and Napanee rivers are used by several species for spawning. Short freshet streams are also used by spring-spawning species. Spawning also occurs in marshy areas: northern pike (*Esox lucius*) and carp (*Cyprinus carpio*); on gravel shoals: in the past for lake whitefish (*Coregonus clupeaformis*), and lake herring (*Coregonus artedii*) and up to the present for smallmouth bass (*Micropterus dolomieui*); and among weed beds: largemouth bass (*Micropterus salmoides*), brown bullhead (*Ictalurus nebulosus*), bowfin (*Amia calva*), and longnose gar (*Lepisosteus osseus*).

Migrations from the St. Lawrence River and from Lake Erie enhance fish species diversity in the bay. American eel (*Anguilla rostrata*) and muskellunge (*Esox masquinongy*) migrate from the St. Lawrence River to the bay. The extinct blue pike (*Stizostedion vitreum glaucum*) and white bass (*Morone chrysops*) were thought to originate from Lake Erie (Christie 1972). Other migrants are quillback (*Carpiodes cyprinus*), various redhorses (*Moxostoma* spp.) and mooneye (*Hiodon tergisus*).

Two other species, now extinct, frequented the bay in earlier times — Atlantic salmon (*Salmo salar*) and lake sturgeon (*Acipenser fulvescens*).

Extensive surveys in the past few years using trap nets, seines, gill nets, and trawls show that 30 species of fish spend at least part of the year in the bay. Only a few of these, however, are especially significant because of their size, number, and/or value to human society.

Percids in the bay include walleye (*Stizostedion vitreum vitreum*), johnny darter (*Etheostoma nigrum*), yellow perch (*Perca flavescens*), and logperch (*Percina caprodes*).

The coregonines were formerly represented by lake herring and lake whitefish but in recent years their numbers have been greatly reduced.

Six species of centrarchids are found in the bay. Until the early 1950s they contributed significantly to the commercial and sport fishery.

Ictalurids are represented by brown bullhead and channel catfish (*Ictalurus punctatus*), both of which are important components of the commercial fishery.

Alewife (*Alosa pseudoharengus*) and gizzard shad (*Dorosoma cepedianum*) are the only clupeids in the bay. Alewife are extremely numerous in the summer months, while gizzard shad numbers have risen markedly in the last few years.

Among esocids, only northern pike are present in any number. Their role as a major piscivore in the

TABLE 1. Morphometric data on the Bay of Quinte and its three distinguishable sections.

	Bay of Quinte	Upper bay (Trenton to Deseronto)	Middle bay (Deseronto to Glenora)	Lower bay (Glenora to Amherst Is.)
Area (km²)	254			
Volume (m³)	2.3×10^9			
Length (km)	86	48	16	22
Width (km)	0.6–5.6	0.6–4.5	0.8–5.6	3
Mean depth (m)	9.1	3.2	6.3	23.8

bay has been a pivotal one, but their abundance has been reduced since the 1930s. Small numbers of muskellunge are present in the lower bay in late summer, but they are not as abundant as they were in the decades before the 1960s (Christie 1965).

Numerous cyprinid species are found in the bay, but carp, which were introduced into Lake Ontario probably in the late 1880s (McCrimmon 1968), is the only commercially exploited species.

Among catostomids, only the white sucker (*Catostomus commersoni*) is frequently taken in significant numbers.

White perch (*Morone americana*) is the only percichthyid found in any quantity in the bay. This species invaded Lake Ontario from the Hudson River drainage (Scott and Christie 1966) and has become the predominant species in the bay in the last 20 yr.

Limnological changes in bay — Evidence of accelerated cultural eutrophication in the bay has been particularly striking since the mid-1940s. Low levels of hypolimnetic dissolved oxygen and high levels of phytoplankton were noticed initially. Beginning in the early 1950s, algal slime increasingly fouled the nets of commercial fishermen. Since the late 1950s, turbidity has increased and the distribution and abundance of aquatic macrophytes have decreased. Concentrations of phosphorus, nitrogen, and several other chemicals have increased during the same period.

The upper bay, because of its shallowness, has always been more eutrophic than the deeper, lower bay. The fact that the major population centers are located on the upper bay has accentuated this difference. The result has been a greater development in the upper than in the lower bay of several of the classic signs of eutrophication: increased algal density, decreased water transparency, and species shifts among most taxa. Table 2 illustrates the current gradation in total phosphorus, total nitrogen, and chlorophyll *a* between the upper and lower bay. The lower values recorded at Trenton reflect the mixing of less enriched water from the Trent River with bay water.

The concentrations of hypolimnetic dissolved oxygen measured opposite Indian Point at intervals since 1945 show a significant decrease in late summer and fall (Table 3), whereas surface water has become increasingly supersaturated during this same period. In other areas of the bay, dissolved oxygen concentrations of less than 3 $\mathrm{mg \cdot \ell^{-1}}$ were recorded near the bottom for periods of 2 mo or more in late summer. Transitory depletions to less than 2 $\mathrm{mg \cdot \ell^{-1}}$ were often encountered near the bottom in the shallow upper bay following several hot, calm days.

TABLE 2. Mean concentrations of total phosphorus and total nitrogen ($\mathrm{TKN + NO_3 \cdot N + NO_2 \cdot N}$) and of chlorophyll *a* from weekly samples in the euphotic zone in the Bay of Quinte from May to mid-October, at seven stations 1972–75.

Station	Total phosphorus $\mathrm{mg \cdot \ell^{-1}}$	Total nitrogen $\mathrm{mg \cdot \ell^{-1}}$	Chlorophyll *a* $\mathrm{mg \cdot m^{-3}}$
Trenton	0.062	0.8043	21.08
Belleville	0.082	0.8477	28.02
Napanee	0.073	0.8667	27.48
Hay Bay	0.053	0.7308	22.48
Picton	0.048	0.6370	18.05
Glenora	0.035	0.5558	13.12
Conway	0.022	0.4446	7.22

Water transparency at Belleville and at Hay Bay has decreased since 1959, particularly in the upper bay (Table 4). Values at both sites tended to be high from May to July and lower in August and September.

The phytoplankton population is dominated by Cyanophyta (blue-green algae) and Bacillariophyta (diatoms). Studies since 1945 show the average concentration of phytoplankton in areal standard units has consistently and substantially increased over the years (Table 5).

Aquatic macrophytes were more abundant and more widely distributed in the bay in the 1880s (Macoun 1888) than they are now (J. M. Bristow personal communication). The only species now common is *Myriophyllum spicatum* (Eurasian milfoil). Macrophyte distribution has become more restricted even since 1959, and in the upper bay most are restricted to small inlets and creek mouths.

Changes in Fish Species Composition and Abundance

Commercial catch statistics provide the best historical record of species changes in the bay

TABLE 3. Values for dissolved oxygen on various dates in 1945 (Tucker 1948), 1964 (McCombie 1967), and 1973 (original data) at two depths at the same station in the lower Bay of Quinte.

	0 m		40 m	
Date	$mg \cdot \ell^{-1}$	% saturated	$mg \cdot \ell^{-1}$	% saturated
1945				
July 17	8.71[a]	97	8.56	80
24	8.71	101	7.85	69
31	8.71	101	7.85	71
Aug. 9	8.85	104	7.14	66
16	9.14	104	7.00	64
29	8.71	99	6.42	58
Sept. 6	9.28	106	6.28	64
29	9.99	101	6.85	69
1964				
June 18	10.00	96	10.00[b]	85
July 16	8.67	94	7.80	68
29	8.87	102	7.00	61
Aug. 14	9.46	98	5.60	51
18	9.73	100	6.33	58
28	9.20	98	5.40	49
Sept. 2	9.80	103	5.53	51
10	9.46	100	3.87	34
17	9.53	98	3.33	30
22	10.46	108	5.00	45
1973				
May 8	11.0	99	10.6	91
June 13	11.8	118	10.0	90
July 5	10.4	119	8.3	75
Aug. 9	9.7	118	6.1	56
28	8.4	98	5.2[c]	45
Sept. 6	8.5	104	4.5	43
18	8.7	93	4.1[c]	36
26	9.8	107	3.3	32
Oct. 2	10.1	105	3.9[c]	36
10	8.9	91	2.0[c]	18
Nov. 29	12.6	102	12.4	101

[a] Converted from $cm^3 \cdot \ell^{-1}$ to $mg \cdot \ell^{-1}$ by multiplying Tucker's (1948) values by the weight of 1 ml O_2 at S.T.P. (1.428 mg).

[b] Samples taken from bottom, at 55 m.

[c] Samples taken at depths of 30–35 m.

TABLE 4. Mean monthly values for Secchi disc readings (cm) at Hay Bay and Belleville in the Bay of Quinte for May through September in various years from 1959 to 1976.

Year	Hay Bay	Belleville
1959	141.8	135.8
1960	125.1	126.4
1963	109.0	87.5
1964	99.8	104.6
1965	111.8	92.3
1972	124.0	109.8
1973	128.3	101.9
1974	118.8	97.6
1975	116.2	89.4
1976	118.6	93.0

TABLE 5. Average concentrations of phytoplankton ($10^9 ASU \cdot m^{-3}$) at various stations in the Bay of Quinte as determined by Tucker (1948) in 1945, McCombie (1967) in 1963–64, Christie (1973) in 1967–68, and K. H. Nicholls (personal communication) in 1972.

	Year			
Station	1945	1963–64[a]	1967–68[b]	1972[b]
Trenton				3.58
Belleville		3.52		5.09
Big Bay			5.96	
Hay Bay		0.75		5.25
Glenora			2.12	2.34
Conway	0.09	0.14	1.31	1.50

[a] Net phytoplankton collected only.

[b] Net and nannoplankton collected.

despite their several imperfections. Some of these imperfections include: delays in new species entering the fishery, fishing effort is directed toward commercially acceptable species, and the absence of sport fish catches.

The total catch was high up to the mid-1940s because of heavy lake herring and lake whitefish catches, but by the 1950s the influence of these species was reduced (Fig. 2). However, the total catch then increased because of improved catches of brown bullhead and catfish, carp, and walleye. In the 1960s and 1970s yellow perch catches increased and the ascendancy of recently colonized white perch (Scott and Christie 1963) created a new fishery that improved the total catch.

For some species we assume that catch trends reflect trends in abundance. Brown bullhead are the principal prey of the hoopnet fishery, which seems to operate independently of market conditions. We have observed, however, that fishing effort does vary with brown bullhead abundance, and this in turn influences hoopnet catches of centrarchids, included in the miscellaneous category (Fig. 2). Christie (1963) noted that catches of lake whitefish and lake herring varied according to weather conditions, but catch averages probably reflected general levels of stock density. The same situation probably applies to walleye and northern pike abundance. However, other species such as yellow perch, American eel, and carp were formerly low value species, and increase in yield was influenced by improved

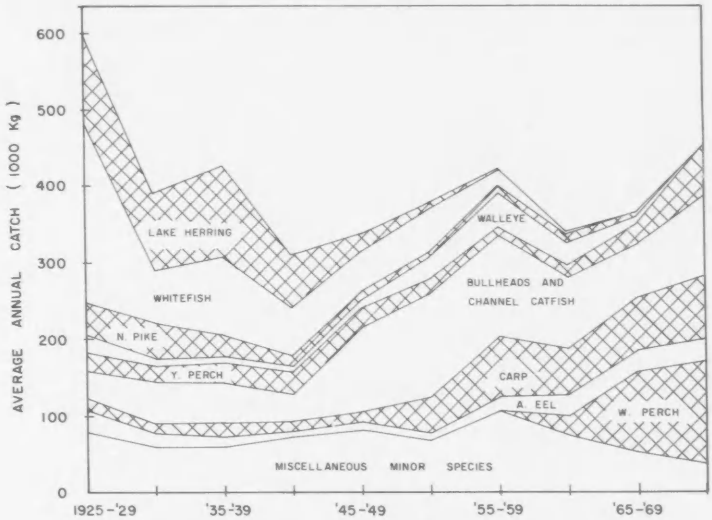

FIG. 2. Annual average catches of major commercial fish species in the Bay of Quinte for 5-yr periods, 1924–74. The top line represents total yields and the contributions of the species are interpolated as band widths.

market conditions and/or scarcity of more desirable species.

Northern pike and walleye were important sport fish up to the mid-1960s so that total yields (Fig. 2) were considerably larger than the data would indicate. A walleye creel census between 1957 and 1966 suggested that in the late 1950s and early 1960s the angler catch nearly equalled the commercial catch (Christie 1965). Catches of northern pike, yellow perch, sunfish, and brown bullhead by anglers have also been extensive, but we have no data on these species.

Experimental gill nets have been used to monitor species composition (Table 6) and although the data cover a shorter time span than those from the commercial catch, they have the advantage of including noncommercial species, and can be used to estimate relative species abundance.

Several trends described by Christie (1972), who cited part of this data set, have been altered by recent observations. Among the percids, walleye remained at a low level of abundance since 1971, and yellow perch showed no trend. White perch increased until 1972 but have shown a falling trend since then. The increase seen in brown bullhead in the late 1960s leveled off in the 1970s. White suckers declined in the late 1960s but appear to have recovered somewhat in the 1970s. Rock bass and pumpkinseed remained at low levels of abundance. Alewife abundance showed extreme year-to-year variations, but recent observations revealed a marked increase. The average number of alewife per net lift for 1958–65 was 310, but for 1967–75 it was 889 — a three fold increase. Gizzard shad also showed a marked increase in abundance from 1969 to 1975, but year-to-year variation has been large for this species also.

Direct Effects of Eutrophication on Fish Stocks

The stress imposed by cultural eutrophication on the composition of fish stocks can best be seen by comparing the Bay of Quinte with a relatively unstressed nearby body of water, West Lake. West Lake is comparable in morphometry and limnology to the bay, and presumably it supports a fish community that resembles that of the bay at an earlier stage in the eutrophication sequence.

The most conspicuous difference in the composition of the catches is the relatively higher abundance of piscivores in West Lake (Table 7). The West Lake catches contained more than twice the mass of piscivores seen at Baker Island (near Trenton at the inner end of the bay) and three times as much as at Hay Bay. Even if alewife, which are virtually absent from West Lake, are excluded as transients in the bay catches, the relative percentages of piscivores for the bay stations are still only 14 and 8, respectively.

TABLE 6. Average numbers of fish of various species caught per lift of a standard experimental gill net[a] at Hay Bay, June–August, 1958–75.

Species	1958	1959	1960	1961	1962	1963	1964	1965	1967
Alewife	68.1(9)[b]	364.3(9)	440.5(10)	160.4(7)	571.5(6)	151.1(7)	108.8(4)	616.7(3)	551.5(4)
Gizzard shad	0.2	0.1	0.1	0	0.3	0.9	1.0	0	0
White sucker	17.8	41.6	18.7	17.6	23.3	13.1	6.3	5.3	3.0
Rainbow smelt	0.1	0.9	0.2	0.3	1.7	5.4	0.5	0.7	6.0
Northern pike	1.0	0.3	1.2	1.1	0.3	0.1	0	2.7	0
Carp	0	2.4	12.5	0.4	1.0	0.1	0.5	0.7	0
Brown bullhead	5.7	6.1	5.7	9.9	26.5	8.1	4.5	13.3	10.5
White perch	151.6	262.7	180.1	37.0	263.5	335.2	160.2	614.0	186.5
Yellow perch	151.2	163.4	221.1	192.6	295.0	207.7	119.5	202.7	209.0
Walleye	13.5	36.9	20.1	34.9	31.0	17.8	12.2	(71.3)[c]	0
Smallmouth bass	5.8	8.2	7.6	3.3	2.3	1.1	1.8	3.3	0
Pumpkinseed	4.4	3.3	16.8	4.0	0.5	0.5	0	5.3	0
Rock bass	10.0	3.3	8.8	2.9	6.3	0.9	0.5	2.0	0

Species	1968	1969	1970	1971	1972	1973	1974	1975
Alewife	304.5(4)	988.0(4)	207.3(3)	521.6(6)	593.3(3)	2283.3(3)	1228.7(3)	1324.7(3)
Gizzard shad	0	10.5	4.0	5.7	20.0	87.3	0	30.7
White sucker	7.5	1.0	8.0	10.7	4.7	5.3	3.3	12.7
Rainbow smelt	1.5	1.5	2.0	0.3	0	6.7	2.7	4.7
Northern pike	1.5	0	0	0.7	4.0	2.0	0.7	1.3
Carp	1.0	0	0	0.3	0	0	0	1.3
Brown bullhead	63.5	17.5	22.7	64.7	22.0	22.0	15.3	36.0
White perch	232.5	778.0	648.7	643.0	746.7	448.7	374.0	137.3
Yellow perch	183.5	113.0	121.3	362.7	234.7	134.7	131.3	217.3
Walleye	22.0	9.5	0.7	1.0	4.7	4.7	2.0	0.7
Smallmouth bass	2.5	1.0	0	5.3	4.0	2.7	1.3	2.0
Pumpkinseed	5.0	0	1.3	10.3	1.3	1.3	0	0
Rock bass	1.0	(20.0)[c]	0.7	0.4	1.3	0	0.7	0

[a] 91.4 m of 3.81, 5.08, 6.35, 7.62, 8.75, 10.16, and 11.43 cm mesh (stretched measure). Values are arithmetic averages for the 3 mo. No data for 1966.

[b] Number of gillnet lifts.

[c] Exaggerated by one unusually heavy catch.

The piscivore value for West Lake is a conservative one. White perch, for example, are very large and fast-growing in West Lake (Hurley 1977). The data of Leach (1962) suggest that between 30 and 60% of white perch in West Lake should be piscivorous, whereas in the bay only 12% grow beyond invertebrate-feeding size range.

We consider that alewife failed to become established in West Lake because piscivore density was high enough to prevent it. West Lake is open to Lake Ontario, where alewife are abundant and lake herring, walleye, yellow perch, and American eel migrate freely. Because of the high piscivore density, white perch have been kept at low density and maintained a high growth rate even though they presumably invaded West Lake at the same time they invaded the bay (Scott and Christie 1963). In the bay, on the other hand, the postinvasion biomass of white perch expanded continuously until recently, but the average size at each age fell significantly (Hurley 1977).

Northern pike abundance in the bay has been reduced by low water levels, which will be discussed later, and by high fishing intensity. But it is significant that the return of higher water levels in the mid-1970s has not resulted in their resurgence. Walleye continue to be abundant in West Lake in spite of considerable fishing pressure but have failed to return in numbers to the bay even after fishing pressure relaxed. Yellow perch, however, were not significant in catches from West Lake but were more abundant in the Bay of Quinte. Figure 2 shows little long-term shift in the commercial catch of yellow perch in the bay until the 1970s, when their numbers increased.

It is unfortunate that there are no data with which to assess earlier trends in the abundance of the other piscivores, largemouth bass, longnose gar, and bowfin, in the bay. Our assumption

TABLE 7. Average trapnet catches (kg) per net-night (6 concurrent nights in July of 1969, 1970, 1971, and 1976) at one West Lake and two Bay of Quinte sampling stations.

	Average Catch		
		Bay of Quinte	
Species	West Lake	Baker Is.	Hay Bay
Piscivores			
Bowfin	3.91	2.07	1.50
Longnose gar	0.17	0	0.32
Northern pike	4.62	0.02	0.39
Muskellunge	0.04	0	0
Walleye	4.46	0.19	0.52
Largemouth bass	0.16	0	0
Channel catfish	0	2.85	0.16
White bass	1.72	0	0.10
Total	15.08	5.13	2.99
Planktivores			
Alewife	0.11	20.11	7.36
Golden shiner[a]	0	<.01	<.01
Herbivore			
Gizzard shad	0.04	0.04	0.22
Miscellaneous benthos feeders			
White sucker	0.26	1.28	0
Brown bullhead	1.72	3.45	0.93
American eel	0.72	0.76	0.98
White perch	18.04	21.68	26.40
Rock bass	1.50	0.09	0.33
Pumpkinseed	2.92	1.60	2.24
Black crappie	10.39	0.85	0.56
Bluegill	14.63	0.08	0.06
Smallmouth bass	1.62	0.46	1.77
Yellow perch	0.03	1.32	0.75
Carp	0	0.28	0
Total	51.83	31.85	34.02
Grand Total	67.06	57.13	44.59
% Piscivores	22.5	9.0	6.7

[a]Biomass not included in total.

is that, though they may have been subject to significant fishing pressure prior to 1950, it was the additional stress of cultural eutrophication beginning in the early 1950s that resulted in their recent low abundance. As none of these species was significant to the commercial fishery, it is not remarkable that fishermen did not comment on trends in their abundance. By contrast, black crappie (*Pomoxis nigromaculatus*) and bluegill (*Lepomis macrochirus*), which are commercially important and now far less prominent in Bay of Quinte catches than in West Lake, are remembered as formerly being much more important to the bay fishery.

Cultural eutrophication is more severe in the bay than in West Lake because there are no major sources of municipal or industrial pollution in West Lake. Although there are some differences in water chemistry between the two areas, the greatest differences are in phytoplankton and macrophyte densities. In West Lake macrophyte composition is more varied and their numbers are extremely high compared with the Bay of Quinte. Phytoplankton density, as judged by chlorophyll *a* values, is greater in the bay than in West Lake. In recent years the average chlorophyll *a* concentration in West Lake is 8.2 $mg \cdot m^{-3}$ while at the same time near Trenton in the bay it is 18.2 $mg \cdot m^{-3}$ and in Hay Bay it is 23.5 $mg \cdot m^{-3}$. We conclude that excessive loads of nutrients in the bay have resulted in additional stresses that impaired piscivore production. This change, in turn, precipitated the sequence of on-going disruptions in the Bay of Quinte species composition.

Interpretation of Shifts in Fish Species Associations

We identify (Fig. 2, Table 2) the following major events in the species composition sequence in the Bay of Quinte since the mid-1920s:

1930s: walleye are low in abundance; northern pike decline.

1940s: lake herring decline; walleye begin to increase.

1950s: white perch invade; walleye become major piscivore; minor northern pike recovery; reduction of largemouth bass, longnose gar, bowfin stocks; reduction of smallmouth bass stocks.

1960s: white perch become predominant; walleye collapse; lake whitefish collapse.

1970s: alewife increase in abundance; gizzard shad increase in abundance.

Christie (1972, 1974) associated the loss of the lake herring with the proliferation of the rainbow smelt (*Osmerus mordax*). Since lake whitefish and lake herring formerly spawned in the same areas, and their larvae even schooled together in the early weeks of life (Hart 1931), it seems possible that lake herring juveniles suffered either by predation or by competition with the rainbow smelt in the lower bay after they became pelagic, and spatially separated from lake whitefish juveniles.

Beginning in the 1920s the lake whitefish stock of the bay was the most important in Lake Ontario (Christie 1963). The fact that it continued to reproduce successfully until 1955 was taken as evidence that the eutrophication stresses had

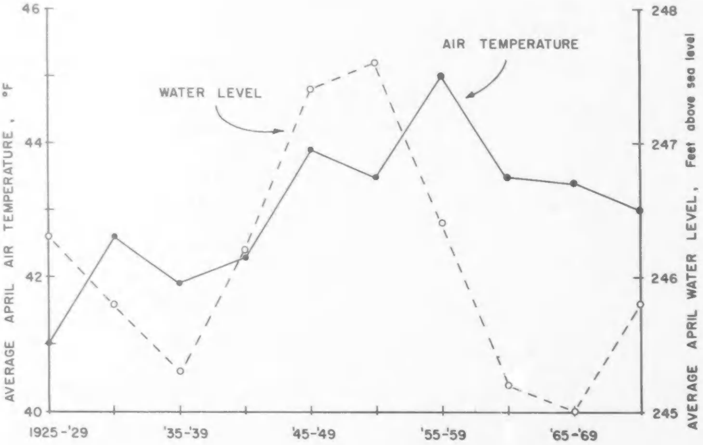

FIG. 3. Average water levels of Lake Ontario in April at Kingston and Oswego, and mean air temperatures for the Bay of Quinte area in April measured at Belleville. Data in both cases are annual averages for 5-yr periods.

TABLE 8. Stomach contents of walleye of various lengths from the Bay of Quinte taken in gill nets between June and end of September, 1958–62.

	Fork length (cm)				
Food item	12.7–25.2 (29)[a]	25.3–37.9 (167)	38.0–50.6 (440)	50.7–63.3 (79)	63.5+ (6)
Alewife	10.3[b]	39.5	60.4	50.6	18.8
Rainbow smelt		4.8	1.1	1.3	
Yellow perch			0.7		
White perch			0.2		
Minnow	3.4				
Unidentified fish	82.8	56.3	42.5	51.9	81.2
Fish eggs			0.7	1.3	
Insects	6.9				

[a] Number of fish that had food in stomach.

[b] Totals may exceed 100% because more than one food type could be present.

not reached critical levels at least until then. Subsequent degradation of the reproductive environment and the explosion of the white perch were considered sufficiently important factors to ensure the stock would not recover. But pressures on the population were severe before the collapse by reason of mortality imposed by overfishing and the sea lamprey (Christie and Regier 1973).

We suggest that northern pike may have collapsed because of fishing pressure combined with low water levels (Johnson 1956) in the mid-1930s (Fig. 3). Cultural eutrophication at that time was not serious. As stated above, algal slime was not noticed until the early 1950s, and the dense macrophyte beds were not affected until the late 1950s. Further, the period of the northern pike collapse pre-dated the effects of the two major invading species.

Although the rapid increase in numbers of walleye after 1945–50 cannot be adequately explained, two circumstances presumably favored it. First, decline in northern pike freed food reserves for walleye. Walleye depended heavily on alewife for food (Table 8). Northern pike, on the other hand, were not so restricted in diet, but the alewife was a significant food item before increasing white perch stocks became an important item in the northern pike diet (Table 9). In addition, the general decline in other piscivores such as longnose gar, bowfin, and largemouth bass, which we presume occurred in the 1950s, released large quantities of alewife

TABLE 9. Percentages of identified fish food items in stomachs of northern pike taken in gill nets set in the Bay of Quinte, 1958–64 (from Tedla 1969).

Identified fish food item	1958 (14, 48.3)[a]	1959 (4, 30.8)	1960 (14, 58.3)	1961 (33, 54.1)	1962 (28, 68.3)	1963 (36, 76.6)	1964 (2, 50.0)
White perch	18.2		7.1	34.8	48.0	84.1	100.0
Yellow perch	27.3		35.7	4.3	8.0	5.3	
Trout-perch		75.0	21.4	34.8	16.0	5.3	
Alewife	54.5	25.0	14.3	17.4	28.0		
Rainbow smelt			21.4				
Rock bass				8.7		5.3	

[a] Number, and percent of northern pike examined that contained fish in the stomachs.

that could be used as forage. Forney (1977) cites a similar decline in piscivores in Oneida Lake as being largely responsible for increases in walleye stocks there.

Secondly, climatic change may have favoured increased walleye abundance. The period 1925–45 was characterized (on the average) by late springs, whereas the frequency of warm Aprils has remained high ever since then (Fig. 3). Busch et al. (1975) showed a high degree of correlation between year-class strength of Lake Erie walleye and the rate of water warming in the spring. Payne (1963) found a nonsignificant but suggestive correlation between estimates of year-class strength of Bay of Quinte walleye and air temperatures in April, the period of egg incubation and early larval life. The air temperatures themselves would be less sensitive indicators of environmental conditions than water temperatures, and this may have acted to blur the effect in Payne's data. The combination of warmer temperatures and the increased forage availability would represent a substantial environmental improvement for walleye.

Our thesis that the piscivores were reduced by the effects of eutrophication rests on the assumption that these effects were selectively deleterious, since walleye and lake whitefish continued to reproduce successfully through the 1950s. It is noteworthy that the affected piscivores are all associated with macrophytes, whereas walleye and lake whitefish are not to any significant degree at any life history stage (Hart 1931; Forney 1977).

As noted earlier, white perch presumably proliferated by reason of the reduction in numbers of predators in the years after their invasion. Their ascendancy coincided and may have been associated with the centrarchid declines. The white sucker decline may have been related also to decline of predators but it is equally likely that the reduced spring run-off associated with the low spring water levels of the 1960s (Fig. 3) constituted a severe impediment to successful reproduction. Yellow perch in the Bay of Quinte appear to be common associates of white perch during the summer period and like white perch seem to be opportunistic invertebrate feeders (Leach 1962). However, the density of yellow perch was evidently unaffected by the increase in white perch density (Table 2). Sheri and Power (1972) suggested yellow perch had been affected, but their data series only extended to 1966, and subsequent observations cancelled the short-term trend. Growth rate of yellow perch was slow throughout the period of study, but here also, no trend can be seen in the size-for-age-relationships.

The collapse of the walleye in the 1960s coincided with the rapid expansion of white perch stocks. There is no direct evidence of white perch predation on walleye eggs or larvae, but Leach's (1962) analysis showed the species to be opportunistic. It may be significant that the species feeds actively in the spring at the time of the walleye hatch and when adult yellow perch are occupied with spawning. That the other factors mentioned may also have been important is not disputed. It seems clear, however, that the aggregate of stresses must have been overwhelming in that period.

The recent prominence of pollution-tolerant gizzard shad seems an entirely natural event in this degradation succession, especially since the adults feed on phytoplankton. Whether the decline of the last major piscivore contributed to this prominence is not known; the circumstantial case is that the late 1960s certainly offered an advantageous environment for gizzard shad.

Lake Ontario–Bay of Quinte Interactions

The present analysis indicates that the main lake and the Bay of Quinte should not be regarded as two productivity subsystems. We consider that the alewife represents the chief vector for materials transport from the lake to the bay and its role has been enhanced by species changes

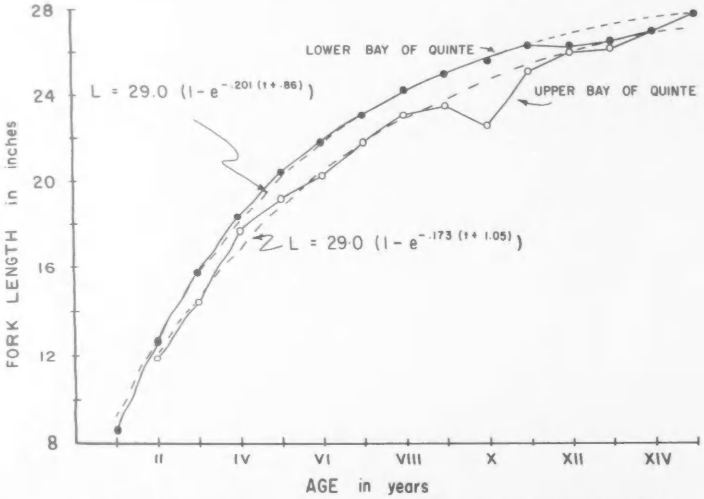

FIG. 4. Fork lengths at various ages for walleye from two parts of the Bay of Quinte, lower bay 1957–62, upper bay 1959–61. Solid lines represent empirical data, broken lines represent mathematically fitted curves (from Payne 1963).

in the lake. The recent gains in fish yield in the bay probably arose because of the destruction of piscivores in the main trench of Lake Ontario.

Up to the early 1960s the most significant known annual movements to and from the bay were those of the lake whitefish and lake herring. These species contributed a significant amount to the commercial yield. Yield here does not necessarily reflect contribution to bay productivity. On the one hand, the adults produced large quantities of eggs and juveniles, which became food for other fishes. The surviving juveniles on the other hand inhabited the lower bay for at least a year (Hart 1931; Pritchard 1931), when they exploited the nutrients of the bay, and the adults cropped bay forage at maintenance levels through the falls and winters.

It was something of a paradox that the walleye should leave the bay as the alewife were entering it, in view of the apparently specialized feeding habits of the walleye. We have no information on the lakeward feeding habits of walleye, but alewife are abundant there in summer also and at that time are about the only available forage. The rich food source produced an excellent growth rate in walleye from the lower Bay of Quinte in the early 1960s (Fig. 4). The slower growth of walleye in the upper Bay of Quinte was attributed to a slow start in somewhat more crowded conditions (Fig. 4). From tag returns the walleye population older than age II was estimated in 1958 at about one million fish, so the supporting population of alewife must have been large to sustain such growth.

The white perch also acts as an importer of energy but its effect may not be as profound as that of the walleye. Each winter we have observed that the bay stocks (and possibly some from elsewhere) congregate at the mouth of the bay. The concentrations are very heavy and support virtually the only commercial fishery, which produces as much as 100,000 kg in three months each year. This behaviour is reminiscent of that of white perch, which inhabit Atlantic seaboard streams and descend to the estuaries in winter (Thoits 1958). The attraction of that area at that time of year is not understood, but their sojourn there no doubt means that they are maintained to some extent by organisms which are produced in part by the intrusions of Lake Ontario water, and this must represent some economy to the productivity of the bay.

The spawning runs of alewife, as noted above, enter the bay in heavy concentrations each year. Their offspring remain for about 1 year and return to the lake for a full year. In the lake they retreat to deep water during the winter. The heavy mortalities often seen along the Lake Ontario shores in spring (Graham 1956) seldom occur within the bay, suggesting that the fish which reach the bay have become acclimated in the warmer waters of the eastern outlet basin. As noted earlier, both juvenile and adult alewife in the bay provide food for northern pike and walleye. Presumably many other resident fishes prey on the juvenile alewife.

We have no data on historical trends in alewife abundance in Lake Ontario. However, the frequency and magnitude of the spring mortalities are probably related to the general levels of alewife density. Certainly Pritchard (1929) and Graham (1956) both described mortalities which were of magnitudes seldom seen in recent years. Possibly alewife abundance varied inversely with the abundance of ciscoes (*Coregonus* spp.) which were the only other main lake planktivores. This would suggest alewife abundance dropped during the 1930s with increasing abundance of ciscoes, and then rose in the late 1940s after the crash of the ciscoes. This increase would have also been supported by the collapses of the lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) stocks in the same period.

The post-walleye upturn in total yields beginning in the late 1960s resulted mainly from increased white perch and yellow perch catches (Fig. 2). We previously noted that the white perch biomass increase seemed to happen at the expense of some other competitive species. This increase may at least be partly due to the energy resources released by the collapse of the walleye stocks.

General Discussion

There is no evidence that overfishing played a predominant role in the degradation of the Bay of Quinte fish community. Even in the late 1950s and early 1960s, when walleye were exploited both by commercial and sports fishery, Christie (1966) could find no evidence that these stocks were being overfished. However, we suggest that exploitation had an ancillary effect together with climate shifts in the case of northern pike, and together with eutrophication in the case of lake whitefish.

We infer that cultural eutrophication, which progressed to extreme levels in the last 25 yr, had its chief direct effect on the nonpercid piscivores, possibly because they are more sensitive to an altered habitat. Reduction in water transparency adversely affected aquatic vegetation, which is important for northern pike production (Bidgood 1973). Reduction in aquatic plants in the upper bay particularly was partly responsible for the fall in northern pike stocks. Reduction of other piscivores occurred at this time, but the reasons are not clear. However, largemouth bass, longnose gar, and bowfin are all dependent on macrophytes (Scott and Crossman 1973) which suggests that reduction in macrophytes also adversely affected their numbers as well.

Proliferation of the exotic white perch followed the fall in piscivore density in the bay, and this proliferation occurred apparently at the expense of a number of other species. White perch habitat spans a broad range of conditions (Scott and Crossman 1973), including those associated with increasing eutrophication. We infer, however, that West Lake and Oneida Lake (Forney 1977) supported white perch in the presence of piscivores, whereas the lack of piscivores in the Bay of Quinte permitted the rapid increase in white perch abundance. The result in the bay, therefore, was a secondary rather than a primary effect of eutrophication.

That yellow perch abundance persisted and may even have increased in the face of the proliferation of an apparently strong competitor, the white perch, suggests that yellow perch have a special niche which has not been significantly altered. White perch do not appear to be much more fit than native yellow perch in this instance. This is contrary to Smith's (1972) hypothesis that an exotic species when it becomes more abundant than native species is dominant over, and will displace, native species. We note also that these two species are not obviously spatially separated except in winter.

Sauger (*Stizostedion canadense*) and blue pike were never important in the bay and little is known about johnny darter and logperch numbers. Increased turbidity does not appear to have impaired the yellow perch habitat, whereas it may have done so for walleye. The fact that walleye avoid temperatures over 24°C (R. B. Fitz and J. A. Holbrook unpublished data) would have forced them to deeper, more turbid water, where their vision may not have been sufficient to permit proper feeding.

Alewife provide the link between fish production in the main lake and the bay. In the 1950s they were responsible for the high walleye production. Since the collapse of walleye stocks, alewife continue to contribute to fish yield in the bay and continued increases in alewife numbers suggest the system has not yet equilibrated.

That alewife are net importers of nutrients to the bay seems supported by the correlation between their increase and that of the fish yield. The relationship requires closer study, however. Yield of white perch increased as a consequence of both increased production and fishing effort. However, yield never caught up with the productivity increase and this resulted in stunting in white perch. Moreover, the pathway of nutrient transfer between alewife and white perch has not been established.

The fact that piscivore production in both the open lake and the bay depended on alewife suggests that the two areas cannot be managed as separate subsystems. Current programs to limit phosphorus inputs to the bay and the return to higher water levels have favored northern pike production recently. The return of more piscivores in the bay to crop the alewife and white perch would allow a more manageable fish community to redevelop.

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Changes in Percid Populations and Species Interactions in Lake Erie[1,2]

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NEPSZY, S. J. 1977. Changes in percid populations and species interactions in Lake Erie. J. Fish. Res. Board Can. 34: 1861–1868.

Changes in the percid community of Lake Erie from 1915 to 1975 are delineated mainly from recently published material. Sauger (*Stizostedion canadense*), blue pike (*S. vitreum glaucum*), walleye (*S. vitreum vitreum*), and yellow perch (*Perca flavescens*) are the percids which have been affected by exploitation, eutrophication and the presence and proliferation of colonizing fish species. Changes in habitat, fishing techniques and gear have also affected percid and nonpercid interactions.

Yellow perch, presently the most abundant percid, have experienced irregularity in recruitment, lack of strong year-classes, and increased exploitation. The concern over the status of yellow perch and walleye has led to some important management initiatives. Improved regulation of exploitation and present efforts by United States and Canadian government agencies to improve Great Lakes water quality, are expected to improve the success for long-term maintenance of percids in Lake Erie.

Key words: Percidae, populations, Lake Erie, habitat change, exploitation, management, *Stizostedion vitreum vitreum*, *S. canadense*, *S. vitreum glaucum*, *Perca flavescens*

NEPSZY, S. J. 1977. Changes in percid populations and species interactions in Lake Erie. J. Fish. Res. Board Can. 34: 1861–1868.

Utilisant en grande partie le matériel publié récemment, nous décrivons les changements qui se sont produits dans la communauté de percidés du lac Erié de 1915 à 1975. Le doré noir (*Stizostedion canadense*), le doré bleu (*S. vitreum glacum*), le doré jaune (*S. vitreum vitreum*), et la perchaude (*Perca flavescens*) sont les percidés qui ont été affectés par l'exploitation, l'eutrophisation et la présence et la prolifération d'espèces de poissons colonisateurs. Des changements dans l'habitat, les techniques et les engins de pêche ont également affecté les interactions des percidés avec les non-percidés.

La perchaude, le percidé présentement le plus abondant, a subi un recrutement irrégulier, une absence de classes d'âge abondantes et une exploitation accrue. La préoccupation causée par la condition de la perchaude et du doré jaune a conduit à d'importantes initiatives de gestion. Une meilleure réglementation touchant l'exploitation et les efforts actuels des organismes gouvernementaux des Etats-Unis et du Canada en vue d'améliorer la qualité de l'eau des Grands lacs devraient contribuer à un meilleur succès du maintien à long terme des percidés dans le lac Erié.

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LAKE Erie centered at 42°15′N and 81°15′W is 388 km long, has an average width of 70 km (92 km at its widest point) and a surface area of about 25,690 km^2 (Table 1).

Much of the lake is shallow and its natural division into three basins (Fig. 1) is of considerable ecological importance. The western basin has many shoals and has been considered to have the most important fish spawning and nursery grounds. Because of its shallowness, heavy use for recreation, and its proximity to large industrial areas like Detroit, Toledo, and Windsor, it is more vulnerable to change from man's activities than the other basins.

Along the north shore and inland areas, agricultural activity is intense and there are few large centers of population or intensive industrialization. The watershed along the south shore is very narrow except at the western end where agricultural land use is also intense. In addition, there are several large population centers with related heavy industrial development.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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TABLE 1. Morphometry of Lake Erie (after Hartman 1973).

Characteristic	Basin[a] Western	Central	Eastern	Whole lake
Maximum length (km)	80.5	213.2	136.8	387.9
Maximum breadth (km)	64.4	92.1	76.4	92.1
Maximum depth (m)	20.4	25.6	64.0	64.0
Mean depth (m)	7.4	18.5	24.4	18.5
Area (km^2)	3,276.0	16,177.0	6,237.0	25,690.0
Volume (km^3)	24.2	299.2	151.7	475.1
Shoreline (km)	431.8	504.2	423.7	1,359.7
Percentage of total area	12.8	62.9	24.3	100.0
Percentage of total volume	5.1	63.0	31.9	100.0
Percentage of total shoreline	31.7	37.1	31.2	100.0

[a] Boundaries as in Fig. 1.

With settlement by Europeans in the 1800s, man's first serious effect on the drainage basin came with the clearing of forest and savannas for farmland and increased soil erosion (Trautman 1957). Population in the drainage basin increased from 0.5 million in 1840 to 3 million in 1900 (Beeton 1969) and 11.1 million in 1970 (Sly 1976). With increased human population, effluents from industries and towns flowed into tributaries or directly into the lake in increasing quantities.

The quality of lake water has progressively deteriorated since the 1850s, although conditions were considered generally acceptable until the latter part of the 1930s. The water quality then decreased at an increasing rate, probably because of increases in population, land use activities and detergent use. This increased cultural activity led to the highly eutrophic state and associated extensive anoxic conditions observed (Burns 1976) in the 1970s. Pronounced changes in the Lake Erie environment, increases in productivity and qualitative changes in the benthos and fish populations from 1925 to 1975 were summarized by Hartman (1972, 1973), Regier and Hartman (1973), and Leach and Nepszy (1976). Induced changes in habitat and fishing methods have affected the interactions of percid and nonpercid species.

This paper documents the changes in the major percid populations of Lake Erie for the past 150 yr. The species considered were and/or are primarily of commercial importance and include: sauger, *Stizostedion canadense*; blue pike, *S. vitreub glaucum*; walleye, *S. vitreum vitreum*, and yellow perch, *Perca flavescens*. The changes are examined in relation to the stresses imposed by cultural eutrophication, exploitation, and colonization by other fish species. Interactions of existing percids (walleye and yellow perch) with nonpercids like rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) are also discussed.

Changes in Populations and Current Status of Percids

Sauger — Increased turbidity and fertility caused by land erosion from clearing and cultivation along the south shore presumably contributed to the increased abundance and availability of the light-sensitive sauger to the fisheries of the United States in the 1880s (Regier et al. 1969). Increased turbidity, particularly from plankton and clay erosion, may have improved the requirements for reproduction of this species.

A decline in commercial landings from a peak in 1916 to virtual extinction by 1960 is clear (Fig. 2). However, the confusion concerning the species of *Stizostedion*, especially juvenile stages of walleye and blue pike, and the tendency to land these together with sauger, must be considered when interpreting these statistics. The downward trend in catches appears regular and may reflect a limiting effect of deteriorating environmental conditions. Traditional spawning reefs in Ohio waters (Maumee Bay) were presumably degraded by pollution, siltation, and damming (Regier et al. 1969). Increased fishing effort from 1930 to 1940 and biological characteristics of slow growth and relatively late sexual maturity (Scott and Crossman 1973) probably contributed to the commercial extinction of this species.

Natural hybrids between sauger and walleye may have occurred in Ohio waters (Trautman 1957) since the two species migrated to adjacent spawning areas in western Lake Erie, for example, the Maumee Bay–Maumee River region. Although some reproductive isolation was maintained by different spawning sites and times, the speculation by Regier et al. (1969), that introgressive hybridization and mixing of sauger with

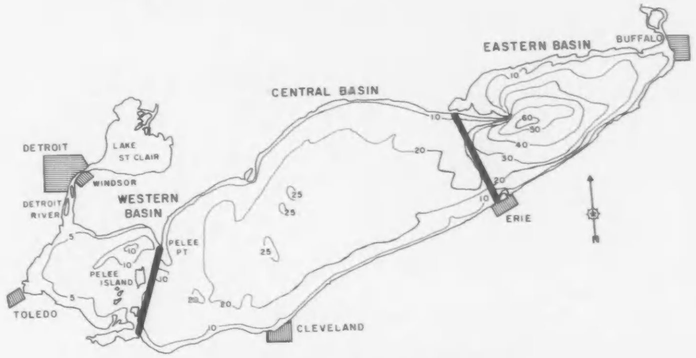

FIG. 1. Bathymetry (m) of Lake Erie.

walleye helped to eliminate remnants of the sauger population warrants further emphasis.

Recent introductions of sauger into Sandusky Bay by Ohio have shown appreciable survival and apparently exceptional growth (R. L. Scholl personal communication). Mature sauger have been observed by commercial fishermen on the Maumee Bay shoals (F. Reynolds personal communication). Present environmental conditions may, therefore, be conducive to survival and growth of this species.

Blue pike — Moderate numbers of blue pike were available to the fishery in the late 1800s and until 1915 (Regier et al. 1969), when production began to fluctuate greatly (Fig. 2). Peaks in production occurred 5 to 9 yr apart with annual production exceeding 9000 t four times and going below 2000 t six times. Greatest production was from U.S. waters until 1950 as well as before 1915. Increased use of trap nets in the 1930–40 period increased production in both countries. With the introduction of nylon gill netting in Canadian fisheries in 1950, exploitation was increased and production surpassed that of the U.S. fisheries (Fig. 2) until the collapse of the fisheries in 1958.

Regier et al. (1969) suggested that the stress of an overintensive fishery disrupted the self-stabilizing mechanisms within the population. They presumed that young-of-the-year blue pike inhabited the same deep and shoal areas as the adults and that they were then vulnerable to cannibalism by older members of the population. However, sufficient information is not available to confirm that cannibalism was the mechanism responsible for the fluctuations from 1915 to 1950. Year-class strength appeared to vary greatly from 1915 to 1943 and did so from 1943 to 1959. The 1944 and 1949 year-classes were the strongest with the last strong year-class produced in 1954 (Parsons 1967).

Despite the lack of recruitment after the strong 1954 year-class, production continued at high levels until 1958. The average age of blue pike in the catch decreased in 1956 and 1957 and then increased markedly in 1958 and 1959 (Parsons 1967). Increased growth rates led to removal of large quantities of immature fish (the 1954–56 year-classes) and thus to reduced recruitment (Parsons 1967).

In addition to the continued intensive fishery, some critical threshold in the accelerating eutrophication of western and central Lake Erie was passed between 1940 and 1945 (Carr et al. 1965). This source of stress may have altered the environment enough to affect the abundance of blue pike and other species. Summer oxygen deficiencies in the central basin hypolimnion probably forced the blue pike to deeper, more suitable waters of the eastern basin, where they concentrated and became more vulnerable to increased fishing effort.

Reasons for the extinction of sauger and blue pike are not entirely satisfactory and adequate explanations may never be found. However, exploitation and reduction of suitable habitat at critical times probably were the greatest sources of stress affecting these stocks. Though introgressive hybridization (Regier et al. 1969) may have been the final factor in the extinction of these percids, the presence of an increasing rainbow smelt population (Leach and Nepszy 1976) possibly taking advantage of an unstable fish community in the mid and late 1950s must have been important in reducing the blue pike population in particular.

Walleye — At the turn of the 20th century, the walleye population in Lake Erie was already a mixture of stocks from many different areas (Regier et al. 1969). Construction of experimental hatcheries along the Lake Erie shoreline in the 1800s initially to propagate lake whitefish (*Core-*

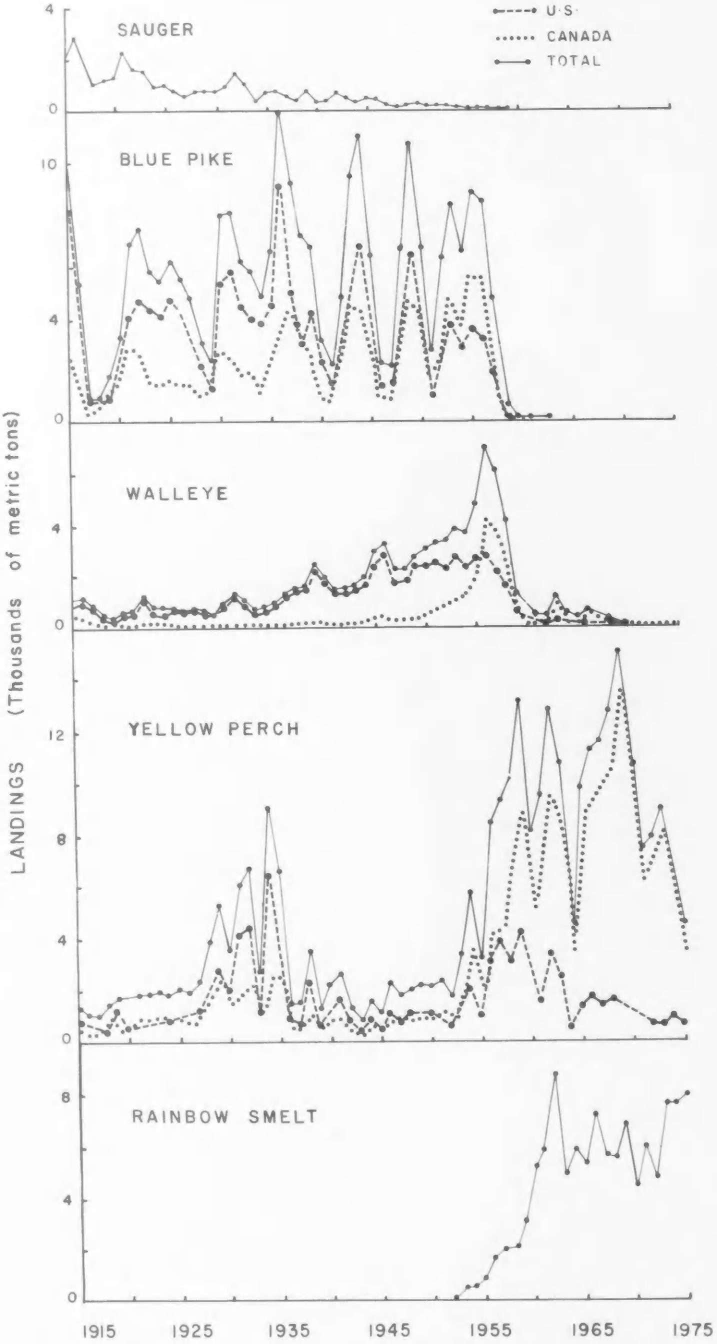

FIG. 2. Commercial landings of four percids and rainbow smelt from Lake Erie, 1915–75.

gonus clupeaformis), permitted the eventual trial and successful raising of walleye eggs. Walleye eggs were obtained from spawning populations in Saginaw Bay, St. Clair River, Thames River, and Maumee River.

Recent studies indicate the presence of at least two discrete walleye populations in Lake Erie: one principally confined to the western basin and the western portion of the central basin and a smaller one in the eastern basin (Wolfert 1963). Very little migration is evident between these two areas but juvenile and mature walleye do move (Ferguson and Derksen 1971) between the western basin, Lake St. Clair, and lower Lake Huron.

Annual landings of walleye fluctuated narrowly about a mean of 825 t between 1915 and 1936 and then increased steadily to 7000 t in 1956 before declining precipitously (Fig. 2). From 1915 to 1956, greatest walleye production was from central and western basin U.S. waters, particularly by Ohio trap netters. Ontario had a small fishery with most landings also from the central and western basins and reaching a peak in 1956. Catches declined in 1958 and 1959 and remained low thereafter.

Reduction in walleye harvest from Canadian waters during the late 1950s was evident in all basins of the lake, although the peak in the eastern basin occurred in 1957, one year later than in other basins. Reductions in U.S. harvests were confined principally to the western and central basins. By the early 1960s, commercial landings of walleye were almost nil from Vermillion, Ohio to Barcelona, New York. In contrast, however, walleye harvest in the most easterly portion of the lake increased from 0.9 t in 1955 to 8.2 in 1956, 5.4 in 1968, and 45.4 in 1975.

The abrupt change in prime producers of walleye from U.S. to Canadian fishermen can be attributed to changes in fishing gear and methods, in quantities of nets fished, in seasonal distrubution of the effort, and in the relative abundance of walleye. The changeover from cotton gill nets to the more efficient nylon gill nets was complete by 1952. By 1955, the effort (yardage) was estimated to have increased fivefold, on the assumption of an increase in net efficiency of 2.5 and a doubling of yardage fished (Regier et al. 1969). The technique of floating or "canning" gill nets near the surface was reintroduced and in general use by the early 1950s. This method increased the efficiency of gill nets in catching walleye.

During the critical years of the rise and fall of the walleye population from 1942 to 1961, year-class contributions varied markedly. Although they were generally strong in the 1942–52 period, they were substantially weaker from 1953 to 1961, except for the 1954 year-class (Parsons 1970). The decline in strength after 1952 was accompanied by a decrease in the number of years during which a year-class was captured by the Ohio trapnet fishery (Parsons 1970). Strong year-classes before 1954 contributed to the fishery for up to 3 yr; subsequent year-classes, for 1 to 2 yr only. The average age of the fish harvested also decreased. With increased growth rates, more of the immature females were taken by the fishery (Parsons 1970), reducing the reproductive potential of the stock. Walleye growth rates have increased markedly since the 1920s, the greatest increases occurring during the mid-1950s and early 1960s (Wolfert 1972).

Cultural and biological sources of stress acting on walleye populations in the western and central basins contributed to the reduced populations there. Environmental degradation altered bottom deposits and produced periodic oxygen depletions, reducing the summer habitat for walleye (Regier et al. 1969). A deleterious effect of the rapidly growing population of rainbow smelt on walleye through competition with and predation on young walleye was postulated by Regier et al. (1969).

Walleye stocks in the western and central basins in 1976 may be at a level similar to that in the early 1950s. This recovery can be partly attributed to strong year-classes in 1970, 1972, and 1974 as well as to closure of commercial fishing in 1970 by Ontario, Ohio, and Michigan because of high concentrations of mercury in walleye.

Suitable environmental conditions, the continued presence of the strong 1970 year-class as well as remnants of mature walleye from other year-classes combined to produce a successful year-class in 1974. This year-class showed strongly in commercial trapnet catches in the fall of 1975 (D. R. Wolfert personal communication) and in experimental gillnet catches in the spring of 1976. Although spawning conditions in the spring of 1975 were not too favorable, the rate of water warming was excellent and the hatch and survival of this year-class was considered above average (R. L. Scholl personal communication). The large brood stock may have offset the unsuitable environmental conditions whereas in the late 1960s, small brood stocks may have been unable to do so (D. R. Wolfert personal communication).

Stability of the adult stock in the eastern basin was evident from the consistent presence of walleye older than those in the western basin stock (Wolfert 1972). However, this may be changing; sampling by the U.S. Fish and Wildlife Service showed that the strong 1971 year-class entered the fishery in 1973 and continued to contribute the greater proportion of seasonal landings. With the removal of this year-class from the fishery, and with the apparent lack of any upcoming strong year-classes, the harvest may be reduced for the short term and the stability of the population may be jeopardized.

Yellow perch — The commercial harvest of yellow perch rose slowly from 1915 to 1927. From 1927 to 1936 landings averaged 5700 t, U.S. landings being much greater than Canadian landings (Fig. 2). This upsurge can be attributed partly to the decline of lake herring (*Coregonus artedii*) as well as to increased effort by U.S. trap netters.

By the 1950s, when the harvest of higher valued blue pike and lake whitefish declined, yellow perch landings increased greatly and became even more important to the fishery. After 1950, Canadian fishermen increased their production and continued to be prime producers of this percid until 1975. Increased effort, increasing use of nylon gill nets, lack of other marketable species (blue pike and walleye), as well as presence of a number of strong year-classes contributed to the increased production in the late 1950s and 1960s. Total landings peaked at 15,286 t in 1969 but declined recently to about 5000 t. Partial and complete bans in 1970 on the taking of white bass (*Morone chrysops*) and walleye, respectively, also increased the fishing effort on yellow perch.

Catch per unit effort (c/f) in the western basin during the productive 1950–70 period was high with low effort. However, after 1970, effort increased in the western and central basin while c/f decreased in all Canadian waters (Great Lakes Fishery Commission personal communication). Effort in U.S. waters for this recent period decreased.

Marked variation in year-class strength has been characteristic of yellow perch populations of the western basin since the 1950s. Strong year-classes were evident in 1952, 1954, 1956 (S. J. Nepszy unpublished data). However, the strong 1959 year-class disrupted this 2-yr periodicity and strong year-classes were produced also in 1962 and 1965 and relatively strong ones in 1970 and 1975.

In the central and eastern basins, sampling of commercial catches and experimental netting by the Ontario Ministry of Natural Resources showed that prominent year-classes were similar to those found in the western basin.

Species Interaction

Much interaction between percids in Lake Erie is evident. Although walleye and yellow perch both spawn in the shallow areas of the lake, walleye prefer sandy, gravelly, or stony shoals (Scott and Crossman 1973). Walleye also seem to remain in loose but discrete schools with separate spawning grounds and summer territories. They prey on yellow perch, freshwater drum (*Aplodinotus grunniens*) or other available forage fish. They can also be highly cannibalistic. Although yellow perch may be a good forage fish for other piscivores, it preys on the eggs and young of a wide variety of fish species.

Rainbow smelt, known to be highly carnivorous on larger invertebrates, feed on sculpins (*Cottus* spp.), young smelt, and other small fish (Gordon 1961; Price 1963; Scott and Crossman 1973). Young-of-the-year assessment (Fig. 3) and commercial landings (Fig. 2) reveal the presence of relatively large quantities of this species so that any predation, on percids in particular, by even a small portion of the smelt population would have some effect.

Coincidental strong year-classes of walleye and yellow perch in 1959, 1962, 1965, and 1970 (Fig. 3) indicate that a similar mechanism may control the success of hatches of these species. Busch et al. (1975) indicated that, for walleye, the rate and regularity of water warming during the spawning and incubation periods during 1960 and 1970 favored egg density and subsequent year-class strength. Similar environmental factors may control the reproductive success of yellow perch.

Pressure from the rapidly enlarging population of rainbow smelt in the 1950s presumably had some effect on walleye year-class success through predation and/or competition (Regier et al. 1969). In the western basin, rainbow smelt spawn a little later than walleye so that post spawning predation by adult rainbow smelt on young-of-the-year walleye and yellow perch is possible. The presence of an alternate year cycle of abundance of rainbow smelt coincidentally with poor year-classes of both walleye and yellow perch (Fig. 3) increases the likelihood of predation as a controlling mechanism. Regier et al. (1969) suggested that, with the close association of yearling and young-of-the-year rainbow smelt in the central basin during the summer (MacCallum and Regier 1970), the yearlings might prey on the young-of-the-year causing an abundance of rainbow smelt every second year. Though rainbow smelt are known to consume their young to a small degree (Gordon 1961; Price 1963), evidence is lacking to substantiate this suggestion. The full extent of this interspecific action on walleye, blue pike, and yellow perch is not known.

Other colonising species like coho salmon (*Oncorhynchus kisutch*) and alewife, whether directly introduced or not, are invading the system, and the extent of interaction with percids is uncertain. Coho salmon feed extensively on

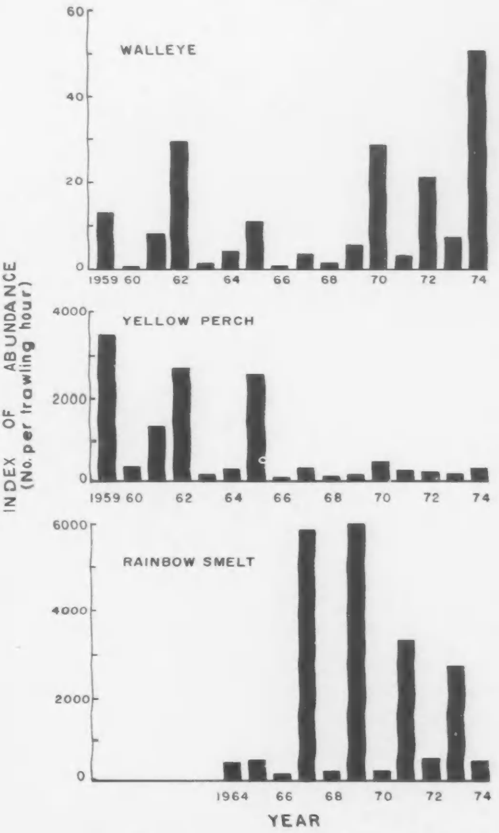

FIG. 3. Relative year-class strengths of young-of-the-year walleye, yellow perch, and rainbow smelt (Redrawn from Leach and Nepszy 1976). Percid data from index trawling in the western basin (courtesy U.S. Fish and Wildlife Service, Great Lakes Fishery Laboratory, Ann Arbor, Mich.). Rainbow smelt data from index trawling (Ontario Ministry of Natural Resources) in the eastern and central basins.

rainbow smelt and emerald shiners (*Notropis atherinoides*). Their continued introduction has been reduced considerably (Great Lakes Fishery Commission personal communication). Introduced salmonids may compete with other predators such as large rainbow smelt and walleye. Alewife have a considerable role to play as a forage base, but mortalities of young-of-the-year and yearlings in 1974 and 1975 (Great Lakes Fishery Commission personal communication) may prevent the expected utilization of this resource in the immediate future. White perch (*Morone americana*), a colonizer in the Bay of Quinte, Lake Ontario and first noted in Lake Erie in 1953 (Larsen 1954) was increasingly evident in western Lake Erie in 1975 with 2–3 year-classes present in sampled commercial catches (W. D. Busch personal communication). Due to the presence of piscivores such as walleye, yellow perch, and white bass, the white perch are expected to be controlled and not proliferate as they did in the Bay of Quinte. The population will probably increase its range and abundance and consequently impose other sources of stress in the form of competition and predation on existing percid stocks.

Management Initiatives

In the early 1970s, increasing concern over the status of yellow perch and walleye in Lake Erie was expressed by agencies managing these resources. The yellow perch resource showed clear signs of stress and deterioration: recruitment levels fluctuated from year to year and no strong year-classes were produced after 1965. The concensus of all agencies in 1975 was that the status of the resource had continued to worsen. The Yellow Perch Committee of the Lake Erie Committee (Great Lakes Fishery Commission), was subsequently formed to develop the technical information required for considering alternative minimum size limits as an interim management measure to help protect and enhance this resource.

Through data analyses and development of models, the effects of alternative minimum size limits on yield, annual biomas production, average stock weight, potential egg deposition, and average spawning frequency were determined and presented to respective agencies together with suggestions for an assessment protocol for evaluating the stock response to such experimental management.

Concern over the status of walleye in western Lake Erie resulted in the formation of a Scientific Protocol Committee (Great Lakes Fishery Commission) in 1973 to develop the technical basis for coordinated scientific management of this resource. The Committee has (1) outlined the methodology for resolving such technical matters as estimation of standing stock, projection of annual surplus production, equitable allocation of total allowable catch, etc., (2) identified basic data requirements in relation to present and future ability to meet them, and (3) suggested protocol for assessment of the resource and surveillance of the fisheries.

Some government regulation is essential if the walleye resource of western Lake Erie is ever to return to a measure of its former importance. Fishing success of the magnitude experienced in the mid-1950s is not anticipated again but some of the factors (fishing effort, environmental conditions) that contributed to those years of abundance have been modified and may now be acting to limit the walleye population.

Acceptance and implementation of some of these recommendations will lead to a more viable and thereby stable fish community. There is assurance in the experiences of some European agencies that have attacked the problems resulting from enrichment and exploitation with more vigor than their colleagues in North America (Nümann 1972; Grimaldi and Nümann 1972). Lake Erie has environmental limitations which preclude the establishment of high-valued fish such as the salmonids suggested by Christie (1974). However, in view of physical location and the present imminent environmental sources of stress, the lake continues to be well suited to the establishment and maintenance of percids (walleye and yellow perch). Although Smith (1972) is pessimistic about the future percid resource in Lakes St. Clair, Erie and Ontario because of degraded water quality, it would appear that present joint efforts between U.S. and Canada to improve water quality in the Great Lakes will achieve some degree of success in the future. Therefore, since the environmental requirements for the maintenance of percids are not as stringent as for salmonids, water quality criteria for long-term success of periods can be achieved.

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Population Dynamics of Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*) in Lake St. Clair, Especially During 1970–76[1]

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JOHNSTON, D. A. 1977. Population dynamics of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in Lake St. Clair, especially during 1970–76. J. Fish. Res. Board Can. 34: 1869–1877.

The fish community in Lake St. Clair has remained fairly stable over the past century despite extensive shoreline modifications, a tenfold increase in population in the drainage area, and exploitation from commercial and recreational fisheries. The lake is productive because of its shallowness and fertile drainage basin. The flushing action of clean water from Lake Huron has restrained deterioration of habitat from euthrophication in most areas.

Annual commercial fishery landings of walleye (*Stizostedion vitreum vitreum*) in the 1960s were five times greater than in the previous 50 yr. The larger catches were due, in part, to increased effort, but also reflect a real increase in the walleye population. In contrast, the sauger (*S. canadense*) declined in abundance through the 1950s and disappeared from commercial landings in the early 1960s. As commercial fishing in Ontario waters of Lake St. Clair was banned in 1970 due to the discovery of high concentrations of mercury in fishes, information on the percid populations was restricted to that obtained from index fishing. Between 1970 and 1976, in association with weak year-classes, the mean age of walleye increased from 2.9 to 5.8 yr. Direct correlations between year-class strength and environmental factors were not evident from the available data. Fishing pressure was reduced considerably after 1970 and is not considered to be an important factor in the low recruitment. The yellow perch (*Perca flavescens*) population showed no evidence of a change in age distribution during the 1970–76 period. The reasons for the reduction in walleye recruitment after 1970 are not clear, but it is possible that the succession of strong year-classes in the 1960s was exceptional and that the recruitment in the 1970s is closer to the normal condition for walleyes in Lake St. Clair.

Key words: Percidae, Lake St. Clair percids, *Stizostedion*, *Perca*, population dynamics, exploitation, community ecology

JOHNSTON, D. A. 1977. Population dynamics of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in Lake St. Clair, especially during 1970–76. J. Fish. Res. Board Can. 34: 1869–1877.

En dépit de vastes modifications à la ligne de côte, d'une augmentation de dix fois de la population dans le bassin hydrographique et de pêches commerciales et sportives, la communauté de poissons du lac Sainte-Claire est demeurée assez stable durant le dernier siècle. Le lac doit sa productivité à sa faible profondeur et à un bassin hydrographique fertile. La chasse d'eau claire en provenance du lac Huron a freiné la détérioration de l'habitat par eutrophisation, comme cela s'est produit dans la plupart des régions.

Les débarquements annuels commerciaux de doré jaune (*Stizostedion vitreum vitreum*) au cours des années 1960 étaient cinq fois supérieurs à ceux des 50 a précédentes. Les prises plus fortes sont dues, en partie, à un effort accru, mais reflètent également une augmentation réelle de la population de dorés jaunes. Par contraste, il y eut déclin du doré noir (*S. canadense*) durant les années 1950, et l'espèce disparut des débarquements commerciaux au début des années 1960. Comme la pêche commerciale dans les eaux ontariennes du lac Sainte-Claire fut interdite en 1970 à la suite de la découverte de la haute teneur en mercure des poissons, nos connaissances des populations de percidés se limitent à celles que nous fournit la pêche expérimentale. Entre 1970 et 1976, par suite de faibles classes d'âge, l'âge moyen du doré jaune augmenta de 2.9 à 5.8 ans. Les données disponibles n'indiquent pas de corrélations directes entre l'abondance d'une classe d'âge et les facteurs de l'environnement. La pression causée par la pêche diminua considérablement après 1970, et on ne la considère pas comme facteur important de faible recrutement. Au

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cours de la période 1970–76, la répartition des âges dans la population de perchaudes (*Perca flavescens*) ne montra aucune signe de changement. Les raisons de la diminution du recrutement de dorés jaunes après 1970 ne sont pas claires mais il est possible qu'un série de classes d'âge abondantes durant les années 1960 aient été exceptionnelles, et que le recrutement des années 1970 se rapproche de la condition normale pour le doré jaune du lac Sainte-Claire.

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THIS paper describes the population dynamics of walleye and yellow perch in Lake St. Clair especially during 1970 to 1976. Information was obtained from angling records, Michigan commercial fishery records up to 1908, Ontario commercial fishery records up to 1970 (Baldwin and Saalfeld 1962 and Supplements), and index fishing records from 1970 to 1976. The monitoring of stocks at index stations was implemented in 1970 after commercial fishing had been banned because of the discovery of high mercury levels in Lake St. Clair fishes.

The fish community is stressed by a moderately intensive fishery, shoreline alterations, nutrient inputs, toxic pollutants, and watershed development. Commercial fisheries existed in both Michigan and Ontario waters until 1908, when Michigan restricted fishing to anglers. Ontario continued to operate a limited entrapment–gear fishery in the lake until 1970.

In the 1950s and 1960s, walleye accounted for more than 50% of the commercial fishermen's income and also was, and still is, the species most preferred by anglers. Sauger was once taken by the commercial fishery, but disappeared from the catches in the early 1960s. Yellow perch was taken by the commercial fishery in substantial numbers but did not contribute the same financial returns as the walleye. The majority of fish caught by angling were yellow perch.

Description of Lake and Adjacent Waters

The lake has a surface area of 1,110 km^2 and a drainage basin of 16,900 km^2, two-thirds of which is in Canada. It has a shoreline of 270 km, a mean depth of only 3 m, a maximum natural depth of 6.4 m and a volume of 3.4 km^3. The mean inflow via the St. Clair River of 5,300 m^3/s is equivalent to about 98% outflow (5,400 m^3/s) through the Detroit River. The theoretical flushing time is about 7.3 days. Other drainage includes flows from the Thames, Sydenham, and Clinton rivers and many smaller rivers and drainage canals. On the Canadian side these waterways drain a large area of intensively cultivated agricultural land.

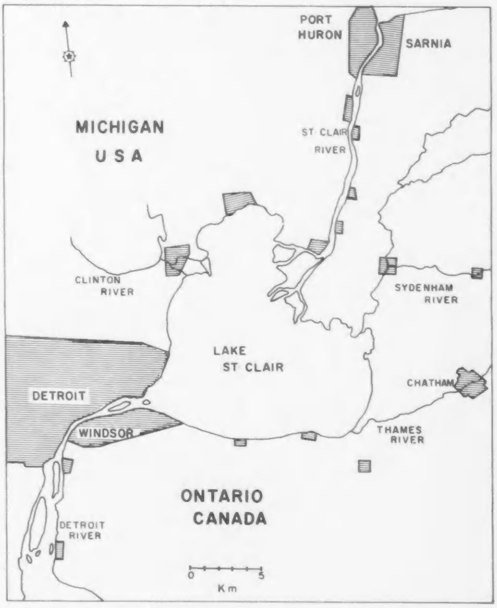

FIG. 1. Lake St. Clair and surrounding areas.

Lake St. Clair lies at the center of the 125 km long waterway between lakes Huron and Erie (Fig. 1). The shorelines of the lake and the St. Clair and Detroit rivers are moderately to heavily developed for residential, recreational, and industrial use. The human population adjacent to the St. Clair system is estimated at 5.5 million. The population in the Lake Erie watershed, which includes the St. Clair system, has increased tenfold in the past century (Beeton 1969; Sly 1976). Approximately 200,000 boats are used for angling and other recreations; estimates of angling effort run as high as one million man-days per year.

There are major chemical industries on the St. Clair River at Sarnia, Ont. The remainder of the river front is primarily residential and recreational except for power stations on each side of the river about 24 km downstream of Sarnia. Loadings of dissolved solids to the river from industrial and municipal sources averaged 750 t/day in 1974 (International Joint Commission 1975).

A major portion of the lake shoreline has been developed for residential or recreational use. Most of the natural shoreline (including 50% of the marsh habitat) on the Michigan side has been replaced by bulkheads and fill materials (Jaworski and Raphael 1976). The Canadian shoreline from the delta to the

Thames River has been modified with dykes. The delta area is owned by the Walpole Island Indian Band and is primarily natural marshland. Shipping channels are dredged regularly to a depth of 8 m.

Frontage on the Detroit River is largely developed for industrial and residential use. Loadings of dissolved solids to the river from these sources averaged 6,480 t/day in 1975 (International Joint Commission 1976).

Glacial history and geomorphology — The glacial origin of Lake St. Clair is similar to that of the Laurentian Great Lakes. The drainage basin was formed by repeated ice advances and under a sequence of glacial lakes which were ponded between the ice sheet on the north and end moraines on the south (Flint 1971).

The St. Clair system is bordered on the Canadian side by the physiographic region of Lake St. Clair clay plains (Chapman and Putman 1951). The prevailing soil type is Brookston clay loam (Richards et al. 1949), which developed under a swamp forest. Drainage is poorly developed and undertiling is necessary to maintain agriculture. Large open ditches and canals drain the tile effluents to the lake or its tributaries. The bird's-foot delta at the mouth of St. Clair River covers about 170 km^2, most of it lying within Ontario.

Limnology — Distribution of nutrients is influenced primarily by the currents in the lake, which are established by the flow of Lake Huron water through the delta system and by wind direction (Leach 1972). Thermal stratification does not occur and dissolved oxygen concentrations are usually close to 100% saturation. In general, gradients in concentrations of chemical variables increase from northwest to southeast. Water quality in the north and central parts of the lake is similar to that of lower Lake Huron.

The phytoplankton community is considered to be a eutrophic diatom association according to the classification of Hutchinson (1967). The spatial distribution of zooplankters showed an increase in abundance from northwest to southeast and was related to the distribution of temperature and chlorophyll *a* content (Leach 1973). In 1973, Leach (unpublished data) found percentages of oligochaetes and chironomids in total benthos to be twice those recorded by Hiltunen (1971) in 1963 and 1965. Percentages of Gastropoda and Pelecypoda had declined in the 1973 survey but percentages of Ephemeroptera and Trichoptera, which require a well-oxygenated environment, were similar in the two surveys.

Little information is available on past environmental conditions. Reighard (1894) did not attempt to determine water quality during his early biological study, but observed that the water lacked transparency. Recent data indicate that, although sulphates and total solids have increased in the past 35 yr, calcium, magnesium, and chlorides have not increased appreciably since the late 1800s (Table 1). The decline in silicate may be due to an increase in silica demand with increasing eutrophication, as suggested by Schelske and Stoermer (1971).

TABLE 1. Concentrations (mg/ℓ) of major ions and total solids at head of Detroit River in various years from 1854 to 1975. Data from Detroit and Windsor water intakes at head of Detroit River (Beeton 1961) except for 1973–75.

	1854	1892	1897	1934–1938	1948–1949	1973–1975
Calcium	20.0	24.8	24.8	27.5	28.0	26.0[a]
Magnesium	—	7.4	6.1	8.0	8.0	8.0[a]
Silica dioxide	5.0	8.9	6.0	7.3	3.8	2.2[a]
Sulphates	6.6	6.7	7.8	12.9	17.4	18.5[b]
Chlorides	—	7.5	—	5.6	6.5	7.5[b]
Total solids	98.1	117.1	114.4	118.6	131.0	136.0[a]

[a] Mean for July–September from Detroit River mouth (Anon. 1975).

[b] Mean for April–November, 1975 from southwestern area of lake (J. H. Leach, unpublished data).

The Fish Community

Lake St. Clair supports a varied fish community of warm water and mesothermic species. Coldwater species are present at times, but are not year-round residents. Many species are at the northern extremities of their ranges and are not found elsewhere in Canada. Some of the more important species are discussed below.

Native species — In the late 1800s, lake sturgeon (*Acipenser fulvescens*) were taken in sufficient numbers in Michigan waters to warrant the building of a sturgeon processing plant. Except for some angling close to the St. Clair delta, there is now no sturgeon fishery. Longnose gar (*Lepisosteus osseus*) are not taken by angling or kept by commercial fishermen, but index fishing indicates a substantial population in the lake. Spring mortalities and experimental gillnet catches indicate a substantial population of gizzard shad (*Dorosoma cepedianum*). Northern pike (*Esox lucius*) are abundant along the north and east shorelines where they were always taken in considerable numbers by the commercial fishery. There is also a limited angling fishery for northern pike. Muskellunge (*Esox masquinongy*) are taken regularly in the summer months by experienced anglers. White sucker (*Catastomus commersoni*) are abundant in the lake. Moxostomids are represented by six species (Scott and Crossman 1973), but mainly the silver redhorse (*Moxostoma anisurum*) and the shorthead redhorse (*Moxostoma macrolepidotum*). Quillback carpsucker (*Carpiodes cyprinus*) are abundant at present; channel catfish (*Ictalurus punctatus*) have always been abundant. Bullhead species (primarily *Ictalurus nebulosus*) are taken by angling, and before 1970 made up a portion of the live fish catch of the Ontario commercial fishery. White bass (*Morone chrysops*) are taken by anglers and were also taken by the commercial fishery.

Bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*) are taken throughout the year by anglers, usually close to weed beds along the north and northeast shorelines. They constitute a major part of the recreational catch in these areas. They were also taken by commercial fishermen. Largemouth bass (*Micropterus salmoides*) are found along the north and eastern shorelines. They are caught by angling but in fewer numbers than the smallmouth bass (*Micropterus dolomieu*). Rock bass (*Ambloplites rupestris*) are taken by anglers over most of the lake. Black crappie (*Pomoxis annularis*) are taken by angling, but not as frequently as the other centrarchids. Freshwater drum (*Aplodinotus grunniens*) are frequently caught and rejected by anglers over most of the lake. The commercial fishery took substantial numbers, but as demand was light many were not marketed. The soft-rayed cyprinids, such as the emerald shiner (*Notropis atherinoides*) and spottail shiner (*Notropis hudsonius*), the troutperch (*Percopsis omiscomaycus*), and the brook silversides (*Labidesthes sicculus*), are important prey for the larger piscivores.

Nonnative species — The sea lamprey (*Petromyzon marinus*) moved through Lake St. Clair when invading Lake Huron, but lack of suitable habitat prevented them from becoming established. Alewife (*Alosa pseudoharengus*) are now abundant. Chinook salmon (*Oncorhynchus* (*tshawytscha*), coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Salmo gairdneri*), and brown trout (*Salmo trutta*) have been planted by Michigan Department of Natural Resources. It is doubtful whether these salmonids will have a major effect on the eastern portion of the lake, although the colder waters of the west may be more favorable and permit populations to exist there. Rainbow smelt (*Osmerus mordax*) are established in the lake. Carp (*Cyprinus carpio*) and to a lesser extent goldfish (*Carassius auratus*) are also well established; the first reports of carp date back to the 1800s and the first complaints to the 1890s. Carp were taken by commercial seine netters along the north and eastern shorelines.

History of the Fisheries

Lake St. Clair supported commercial fishing from the days of the first settlers until 1970. Total effort was extensive in both Michigan and Ontario waters in the late 1800s but declined substantially when the Michigan fishery was banned in 1908.

Michigan commercial fishery — Total Michigan production (including St. Clair and Detroit rivers) peaked in 1890 (Alexander 1904) at almost 1,320 t, but declined to 140 t by 1903. Production of walleye in Michigan peaked in 1891 at 346 t but declined to 45 t by 1908 (Fig. 2). Other species declined even faster, however, so that by 1903 walleye represented almost 75% of the reported catch. Yellow perch landings were also variable, peaking at 377 t in 1881, rapidly falling off to 25 t in 1887 and declining to nil by 1907.

Ontario commercial fishery — The Thames River and, to a lesser extent, the Sydenham River have provided a spring walleye fishery since the time of early settlement. This fishery became increasingly important to non-Indians, who used a variety of entrapment gear until 1950, when the fishery was restricted to angling. The Indian communities adjacent to the Thames River have been allowed limited access to the walleye run with entrapment gear.

Catches of percids from the lake were heaviest in the spring months. Fishing effort increased in February and March during the 1960s, causing part of the rise in reported yield (Fig. 3), but this expansion in effort was also in response to an increase in the walleye population.

Recreational fishery — Summer angling is lakewide, whereas winter fishing is concentrated in the more sheltered bays, on the lower Thames River and along the southeastern shoreline. In two creel surveys, Krumholz and Carbine (1943, 1945) found that yellow perch was the major species caught in the lake and that walleye predominated in the Detroit and St. Clair River fisheries.

Data for the 1950s indicate a substantial winter fishery for yellow perch and walleye along the southeastern shoreline, and a winter fishery for yellow perch in the bays along the north shore. Summer angling was extensive; an aerial count for Ontario waters on one day in May 1957 revealed almost 600 boats with anglers.

Michigan Department of Natural Resources estimated that about 78,000 walleye were caught from June to August in 1966 and 961,000 from April to August in 1967. No comparable data are available from Ontario, but summer fisheries for walleye in the center of the lake were extensive in those years. Michigan Department of Natural Resources estimated that 1,319,000 yellow perch

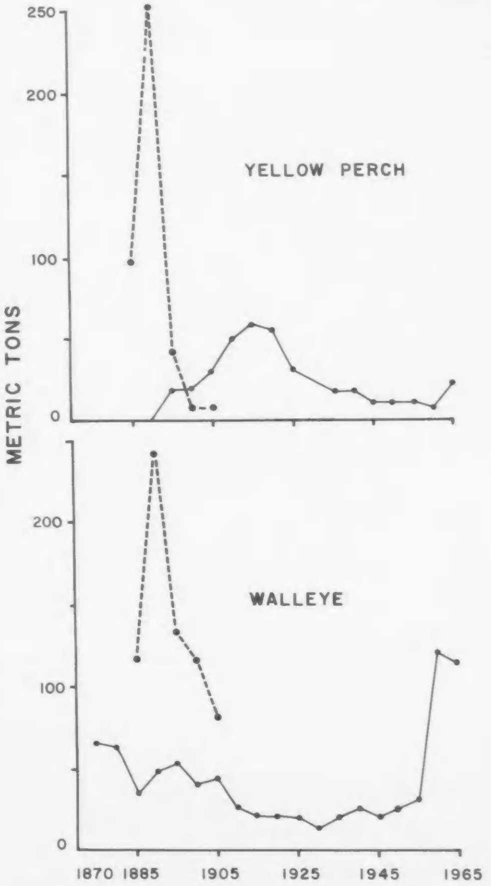

FIG. 2. Commercial fishery yields (5-yr averages in metric tons) in Michigan (dotted lines) and Ontario (solid lines) waters of Lake St. Clair for yellow perch and walleye, 1870–1969 (from Baldwin and Saalfeld 1962 and supplements).

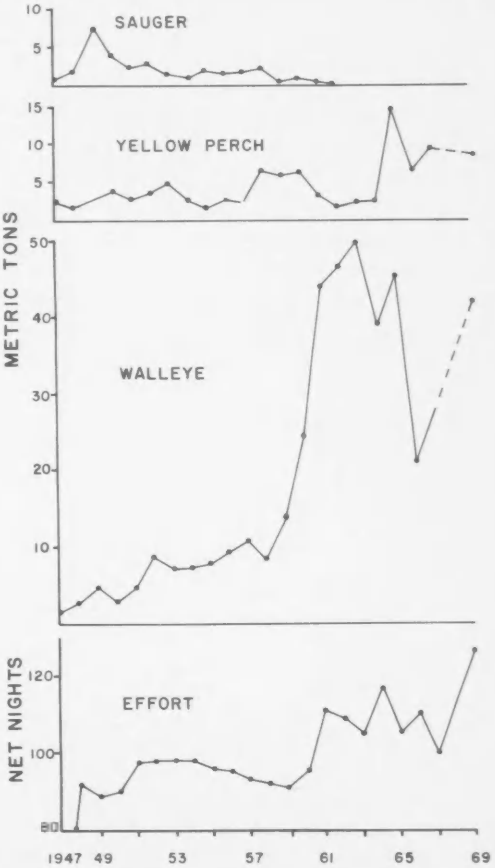

FIG. 3. Commercial fishery yields (metric tons) for selected fisheries in Ontario waters of Lake St. Clair (Baldwin and Saalfeld 1962 and supplements), and effort (number of net nights) used in their capture, 1947–69. Prior to 1947, sauger landings were included with those of walleye.

were caught from June to August in 1966 and 1,455,000 in a 5-mo period in 1967. Ontario records showed that substantial numbers of yellow perch were caught in all areas.

Angling effort in Ontario waters dropped sharply from 533,000 rod-hours in 1969 to 209,000 rod-hours in 1970 (Table 2) due to the publicizing of high mercury levels in Lake St. Clair fish. Effort increased to 461,000 rod-hours in 1974, but dropped again in 1975 to 365,000 rod-hours. I assume that, without the mercury problem, angling effort in Ontario waters of the lake would normally fall between 300,000 and 500,000 rod-hours for the 99-day summer period. Comparable data for this period are not available from Michigan waters.

Estimates of summer landings of walleye in Ontario waters varied from 11 t in 1970 to 30 t in 1973 (Table 2). Most perch were caught incidentally, but still accounted for the majority of fish taken from Ontario and U.S. waters. Estimates of summer landings of yellow perch in Ontario waters varied from 5 t in 1972 to 53 t in 1969 (Table 2).

The winter fishery for walleye is limited to the southeastern shoreline, the center of the lake, and the lower 10–15 km of the Thames River. Success varies greatly between years. A census of the

TABLE 2. Estimates of total angling effort[a] (thousands of rod-hours) for all species, angling yields and success (CUE)[b] for walleye and yellow perch in Lake St. Clair, 1969–75.

	Rod-hours	Walleye			Yellow perch		
		No. × 10^3	MT	CUE	No. × 10^3	MT	CUE
1969	533	37	25	0.169	421	53	1.179
1970	209	17	11	0.373	92	12	0.799
1971	255	18	12	0.342	138	17	1.004
1972	213	28	19	0.332	41	5	0.701
1973	333	45	30	0.286	53	6	0.352
1974	461	41	27	0.180	162	21	0.567
1975	365	25	22	0.152	102	13	0.481

[a] For standard 12-h day and 99-day summer.

[b] Catch (observed number of fish kept) divided by effort (observed number of rod-hours spent seeking that fish).

Thames River in 1973 indicated a substantial walleye fishery. The major yellow perch fisheries are in the northwest and northeast corners of the lake. Even with the poor ice conditions of 1975, Ontario figures showed an estimated 200,000 rod-hours of effort. Yellow perch landings were estimated at 208,000 (25 t). Total yields for 1975 angling in Ontario waters were estimated at 38 t for yellow perch and 27 t for walleye.

Walleye and Yellow Perch Stocks, 1970–76

Data used in the following discussion on percid population dynamics were obtained from modified hoop nets fished at a number of locations in Ontario waters of the lake. These index nets were set for at least 4 wk each fall from 1970 to 1976. The nets had leads of 100 m by 2 m and used three-chambered square pots. Information on angling in both summer and winter was obtained from on-lake "roving type" censuses.

Available data indicate an increase in mean age of walleye caught in index gear from 1970 to 1976. This trend was concurrent with an overall drop in recruitment in comparison with the 1960s. With available data, it is not possible to show cause–effect relationships between walleye year-class strengths and other variables. Yellow perch did not show a trend in age structure.

Walleye — Tagging studies (Ferguson and Derksen 1971; Roseborough 1958; Wolfert et al. 1975) indicated considerable movements of walleye between Lake St. Clair and adjoining lakes Erie and Huron. Each lake has many known and some suspected spawning areas. Since walleyes prefer to spawn close to their place of origin (Eschmeyer 1950; Ferguson and Derksen 1971), there must be a number of semi-discrete stocks coexisting in these lakes. Tagging studies have not been sufficiently intense, however, to delimit these stocks within time and space.

Age-groups as shown (Fig. 4) are assumed optimal in terms of reproductive potential (Savel'yeva and Shuvatova 1972).

Since 1970, when commercial fishing was closed, there have been no apparent changes in stress indicators. If the commercial fishery had exerted considerable stress, indicators such as growth rate and fecundity should have decreased in compensation for the lowered fishing mortality. This has not occurred.

A noticeable trend since indexing began, in 1970, is that the mean size and age of the walleye population have been increasing (Fig. 5). This would be expected since the 1970 year-class was strong (Fig. 4), but the trend has been concurrent with relatively low recruitment. The 1974 year-class, however, made up a substantial part of the spring 1976 angling fishery, indicating a possible check in the sequence of weak classes mentioned above. The conclusion that the walleye population of the 1960s consisted of smaller fish than are now present is supported by observations of commercial fishermen, photographs of their catches, and the ready availability of sublegal (35.6 cm) fish for tagging at that time.

It is doubtful whether angling effort has varied greatly over the past decade except for the decline and recovery in the 3 yr after the mercury crisis in 1970 (Table 2). Catch per unit of effort (CUE) for those seeking walleye declined consistently from 1970 to 1975 (Table 2). This was in part due to an increased number of inexperienced anglers, but was also related to decreased walleye availability due to the overall lower recruitment.

Over the last 30 yr, mean annual water levels of the lake have varied by as much as 1.7 m which has affected volume and mean depth appreciably. Variations in depth can alter macrophyte growth, erosion, and turbidity. Water level fluctuations also have indirect effects, such as necessitating increased channel dredging when levels are low. However, there was no apparent correlation between water levels and year-class strength.

Information for the 1950s indicates considerable pollution of both the Sydenham and the Thames rivers, primarily by high BOD organic effluents. Walleyes were not observed at London in the 1950s at traditional spawning sites and their absence was attributed to the raw sewage originating from that city (Beck 1957). It is not known how the fish were affected farther down-

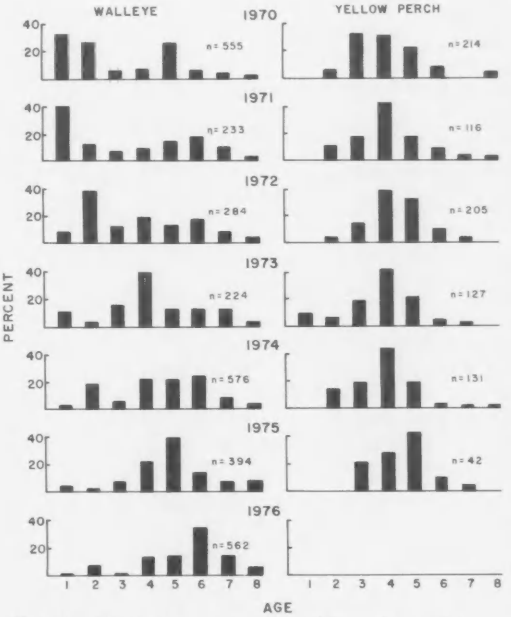

FIG. 4. Percentage age compositions for walleye and yellow perch populations as determined by index fishing from 1970 to 1976.

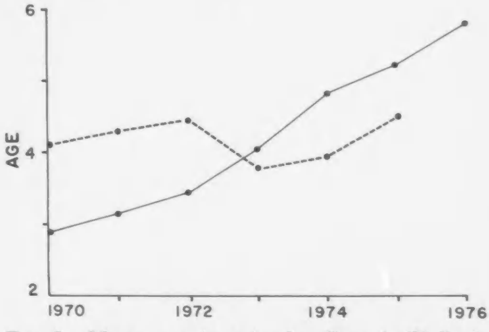

FIG. 5. Mean ages (years) of walleye (solid line) and yellow perch (dotted line) as determined by index fishing from 1970 to 1976.

stream, but presumably dilution was sufficient in the spring to prevent major failures of the spawning run. Conditions have improved in the last decade. The Sydenham River received considerable pollution from Wallaceburg industries in the 1950s (A. H. Berst unpublished data), but water quality has since improved. Recent limnological data for the Thames River in the spring months suggest that the water quality is now adequate for walleye spawning (Ontario Ministry of the Environment, unpublished data). Direct relationships between water quality of the Thames and Sydenham rivers and year-class success over the past decade are not obvious.

"Fit and fat" females produce more viable eggs than those in poor condition (Savel'yeva and Shuvatova 1972). A good growing summer in the year prior to spawning should produce such females. Summers of good growth are normally associated with warm temperatures (Svardson and Molin 1973; Doan 1942) and, indeed, the summers of 1971 and 1973 were above average (J. H. Leach personal communication) and so may have helped to produce the relatively strong year-classes of 1972 and 1974 as determined by young-of-year abundance indices (S. J. Nepszy personal communication). But no obvious correlations can be drawn between spring water temperatures and year-class strengths of walleye in the lake.

After hatching, walleye fry remain pelagic for 2–7 wk (Forney 1966; Eschemeyer 1950). Wind-induced currents in Lake St. Clair (Ayers 1964) could distribute fry from the Thames and Sydenham rivers to areas of the lake with lower productivity (Leach 1972). Prevailing winds are from the southwest and west and these create local circulations within the southeast corner of the lake which would concentrate the fry in areas of maximum productivity. East winds tend to move water away from the southeast and mix it with less productive Lake Huron water. But the average strength and direction of May winds showed no correlation with year-class strength.

Walleye fry and eggs have been stocked in Lake St. Clair and surrounding waters many times, especially in the late 1800s and the 1930s. This stocking has had little influence on the indigenous populations.

The walleye population has remained strong despite the moderately intensive fishing pressure and habitat degradation. Attempts by man to deplete or replenish the stocks have as yet met with little success. Such resilience is probably due to the number of separate spawning populations and the wide range of age-groups, which have effected a momentum to carry the population through years of poor recruitment. The recent decline in recruitment is difficult to interpret when we consider that growth rates are largely unaltered, relative abundance of the older fish is high and hatch success has been relatively strong in some years.

Yellow perch — Yellow perch spawn in most inshore areas of the lake, but it is not known whether discrete stocks exist. Commercial fishermen consider that fish from Lake Huron can be identified by shape and color and that these fish are taken in Lake St. Clair. Also, Ohio fishermen consider that postspawning movements of large yellow perch into the western basin of Lake Erie contain stocks nonnative to Lake Erie. They are presumed to come from Lake St. Clair. There is no evidence to support or reject these views. The scant tagging that has been carried out with yellow perch suggests that they are capable of moving between the lake systems (R. G. Ferguson and R. Cummings unpublished data). However, the maintenance of a number of age-groups in Lake St. Clair (Fig. 4) in direct contrast to the situation in Lake Erie (S. J. Nepszy personal communication) argues against substantial movement (i.e. some mutual diluting of population structure would have been expected had the connection been a major one).

As already suggested for the walleye, if the effect of commercial fishing had been great, we should have expected some changes in the population due to relaxation of that stress after 1970. No such trend was apparent, as the mean age of fish caught in the fall fluctuated about 4+ (Fig. 5). Mean fork length for each age-group and recruitment of yellow perch to the index gear (Fig. 4) also showed no major trends.

A large percentage of the fish caught through the year by angling in the lake are yellow perch. In the winter, yellow perch make up over 90% of the landed fish. The anglers of 1975 landed a greater weight of yellow perch (Table 2) than did the commercial fishermen in any year during the 1960s (Fig. 2).

Information from index gear and angler surveys suggests that the population is still strong in Lake St. Clair. A very good hatch in 1975 supports this view.

Sauger — Regier et al. (1969) speculated that the ultimate reason for the disappearance of the remnant stock of sauger in Lake Erie was its absorption into the walleye gene pool following a period of low abundance. Before 1947, sauger were not segregated from walleye in the commercial returns. Interviewed commercial fishermen relate that, at the end of the 1950s and the first part of the 1960s, sauger began to merge morphometrically with walleye. Landings of sauger declined at the same time as the walleye landings increased (Fig. 3). Sauger are now rare in the lake.

Conclusions

The fish community of Lake St. Clair, with the exception of some coldwater species, has changed remarkably little in the last hundred years despite an expanding human population in the watershed and exploitation from commercial fisheries. I see two main reasons for this. The first is the flushing action of relatively clean water from Lake Huron which has prevented concentration of nutrients and progressive eutrophication in most of the lake. The second is that the commercial fishery, which operated from the turn of the century until 1970, was relatively small and fairly well regulated. Fishing activities were limited by seasons and area allocations; type and quantity of gear were also restricted. The live capture of fish in hoop nets allowed the release of immature and other illegal fish, thereby eliminating the "incidental catch" problem.

The percid populations have always played a major role in the fish community of the lake. Our index data are insufficient for conclusive trend interpretation, but it is possible that the lowering of walleye recruitment represents a return to pre-1960 conditions. The implication is that the 1959 to 1970 series of strong year-classes was the exception rather than the usual, and that we are now returning to a "normal" condition of walleye abundance.

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Walleye (*Stizostedion vitreum vitreum*) Fluctuations in the Great Lakes and Possible Causes, 1800–1975[1]

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Changes in walleye (*Stizostedion vitreum vitreum*) stocks in the Great Lakes from 1800 to 1975 were linked to proliferation of foreign species of fish and culturally induced sources of stress — exploitation, nutrient loading, alteration of spawning habitat, and toxic materials. During the 1800s, three small spawning stocks (and probably many others) were damaged or destroyed because of either overfishing or elimination of spawning habitat through logging, pollution, or damming.

During 1900–40, stocks in the Michigan waters of Lake Superior, southern Green Bay, the Thunder Bay River of Lake Huron, the North Channel of Lake Huron, and the New York waters of Lake Ontario declined gradually. Pollution, in general, and degradation of spawning habitat, in particular, probably caused three of the declines and overexploitation was suspected in two instances. In addition, the decline of three of these stocks occurred when rainbow smelt (*Osmerus mordax*) were increasing.

During 1940–75, stocks in seven areas declined abruptly: Saginaw Bay (1944), northern Green Bay (1953), Muskegon River (mid-1950s), western Lake Erie (1955), Nipigon Bay (late 1950s), Bay of Quinte (1960), and Black Bay (mid-1960s). The decline of each stock was associated with a series of weak year-classes. The stocks were exposed to various sources of stress, including overexploitation, pollution, and interaction with foreign species, which, if not important in the decline, may be suppressing recovery. Only the western Lake Erie stock recovered, in part due to a reduction in exploitation and, possibly, because of the relatively low density of smelt and alewives (*Alosa pseudoharengus*) in the nursery areas.

Relatively stable stocks persisted in five areas: Wisconsin waters of Lake Superior, Lake St. Clair — southern Lake Huron, eastern Lake Erie, northern Lake Huron, and parts of Georgian Bay. Pollution problems were relatively minor in these areas and exploitation was light during recent decades. Apparently these stocks were more capable of withstanding the additional stresses exerted by alien species.

Key words: population fluctuations, Percidae, *Stizostedion*, Great Lakes walleye, history of fisheries, summary of stresses, harvests, management implications

SCHNEIDER, J. C., AND J. H. LEACH. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800–1975. J. Fish. Res. Board Can. 34: 1878–1889.

On attribue les changements qui se sont produits dans les stocks de dorés jaunes (*Stizostedion vitreum vitreum*) dans les Grands lacs de 1800 à 1975 à la prolifération d'espèces de poissons étrangers et de contraintes déclencheées par la culture — exploitation, charges en éléments nutritifs, altération de l'habitat sur les frayères et matériaux toxiques. Durant les années 1800, trois petits stocks reproducteurs (et probablement plusieurs autres) furent endommagés ou détruits soit par surexploitation, soit par élimination de frayères à la suite d'explotation forestière, de pollution ou de construction de barrages.

Au cours de la période de 1900–40, les stocks de la baie Verte méridionale dans les eaux du Michigan du lac Supérieur, de la rivière Thunder Bay du lac Huron, du chenal nord du lac Huron

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et des eaux new-yorkaise du lac Ontario diminuèrent graduellement. La pollution en général et la dégradation de l'habitat des frayères en particulier furent probablement la cause de trois des déclins, et la surexploitation probablement responsable dans deux cas. De plus, le déclin de ces trois stocks se produisit alors que l'éperlan arc-en-ciel (*Osmerus mordax*) augmentait.

Durant la période de 1940–75, les stocks de sept régions diminuèrent abruptement: baie Saginaw (1944), baie Verte septentrionale (1953), rivière Muskegon (mi-1950), lac Erié occidental (1955), baie Nipigon (fin des années 1950), baie de Quinte (1960) et baie Black (mi-1960). Le déclin de chaque stock était associé à une série de faibles classes d'âge. Les stocks étaient exposés à diverses sources de stress, y compris la surexploitation, la pollution et l'interaction avec des espèces étrangères. Ces sources n'ont peut-être pas été importantes dans le déclin, mais elles peuvent empêcher le rétablissement. Seul le stock du lac Erié occidental se rétablit, en partie à la suite d'une diminution de l'exploitation et possiblement à cause de la faible densité de l'éperlan arc-en-ciel et du gaspareau (*Alosa pseudoharengus*) dans les régions d'alevinage.

Des stocks relativement stables persistent dans cinq régions: les eaux du Wisconsin du lac Supérieur, le lac Sainte-Clair–lac Huron méridional, le lac Erié oriental, le lac Huron spetentrional et des portions de la baie Georgienne. Les problèmes de pollution furent relativement mineurs dans ces régions, et l'exploitation a été faible au cours des récentes décennies. Apparemment, ces stocks pouvaient mieux supporter les contraintes supplémentaires exercées par des espèces étrangères.

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IN this paper we review changes in walleye (*Stizostedion vitreum vitreum*) populations in the Great Lakes (Fig. 1) since commercial fishing began in the early 1800s. We give particular attention to fluctuations in abundance induced by the activities of man (exploitation and alteration of habitat) and by interactions with exotic fish, such as rainbow smelt (*Osmerus mordax*), sea lamprey (*Petromyzon marinus*), and alewife (*Alosa pseudoharengus*).

Our procedure was to: (1) summarize trends in abundance for each walleye population and other data needed to identify when major fluctuations in abundance took place and their probable causes (more detailed accounts are given by Schneider and Leach 1977), (2) look for a relationship between changes in walleye populations and the dispersal patterns of exotic fishes, (3) contrast the environmental characteristics of stable and unstable walleye stocks, and (4) draw inferences about the interactions of walleyes with other fish and with man. "Population" refers to a discrete spawning stock or, if the data were inadequate at that level, to the inhabitants of a geographical area.

We relied heavily on the comments of experienced observers and unpublished information in addition to the literature. Trends in abundance of walleye were inferred mainly from descriptive accounts of fisheries in early years and from the commercial catch records in later years. Extensive use was made of (1) highly detailed ledgers of the Michigan State Board of Fish Commissioners, which indicated the locations, nature, and magnitude of the Michigan commercial fishery from 1891 to 1908; (2) commercial fish production records for all the Great Lakes, 1880–1975 (Baldwin and Saalfeld 1962); (3) records of commercial catches by statistical districts for the Ontario waters, 1956–74; and (4) detailed records of commercial catches and effort by statistical districts for the U.S. waters, 1929–69 (commercial walleye fishing was banned in Michigan waters after the 1969 season).

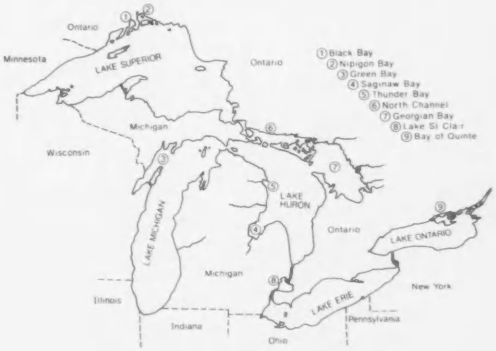

FIG. 1. The Great Lakes.

Lake Superior

The walleye populations of Lake Superior have always been relatively small and widely scattered due to the limited amount of favorable habitat; the highest annual catch (Fig. 2) was only 171 metric tons (t). Most of the walleyes were taken from Black Bay, Ont., but significant populations existed in Nipigon Bay, Ont., and in the inshore waters of Michigan, Wisconsin, and Minnesota.

In 1975, only the population in Wisconsin

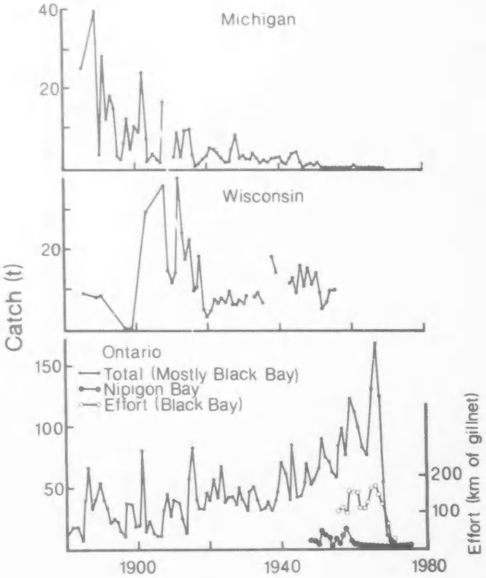

FIG. 2. Commercial catches of walleyes from the Michigan, Wisconsin, and Ontario waters of Lake Superior, 1880–1975, and fishing effort at Black Bay, 1956–75.

waters remained in good health, but even these may be in jeopardy (G. King personal communication). They were protected from commercial exploitation from the late 1950s until recent years. The Black Bay stock collapsed abruptly after the peak harvest in 1966, the Nipigon Bay stock crashed in the late 1950s, the Michigan stocks began a gradual decline at the turn of the century, and the Minnesota stock has been small since it produced a peak harvest of 56 t in 1885. Populations of sea lamprey and rainbow smelt exploded in Lake Superior during the 1950s, but these species probably were of minor importance in the decline of walleyes in Black Bay and Nipigon Bay. Walleyes in Wisconsin waters have coexisted with large numbers of sea lampreys and rainbow smelt for over 20 yr.

Overfishing was the most likely cause for the decline of stocks in Black Bay, Michigan, and Minnesota. In Black Bay, effort greatly increased in the late 1950s and by 1965 only two year-classes supported the fishery (Fig. 2 and R. A. Ryder personal communication). It appears that year-class success was poor in the mid- and late-1960s and, in the absence of adequate recruitment, the population was quickly depleted by the fishery. Along the south shore of Lake Superior, concern about overfishing with pound nets was expressed in the late 1800s (Rathbun and Wakeham 1898). However, it is also possible that the high catches in Michigan and Minnesota in the early years were due to expansion of these stocks to unusually high levels — current levels being more typical. Goode (1884) reported that walleyes were rare in Whitefish Bay until they began to increase about 1868. He also noted that in 1880 fishermen in Wisconsin and Michigan were "deeply puzzled" by an "immense" run of walleyes in the last 2 yr as compared with the previous 4 yr. The increase may have been triggered by the reduction of competitive inshore fishes by fishing, climatic fluctuations, or alteration of habitat by logging.

Pollution from a kraft paper mill probably caused the demise of the Nipigon Bay walleye stock. An increase in fishing mortality from 0.10 in 1955 to 0.39 in 1957 was of secondary importance because adults were present for several years after recruitment ceased (Ryder 1968). Ryder reasoned that effluents from the mill disoriented walleyes so that they did not return to their traditional spawning grounds in the lower Nipigon River and that they found no suitable alternative site. Subsequently, runs of suckers (*Catostomus* spp.) into the river also declined.

Lake Michigan

The largest populations of walleyes in Lake Michigan existed in northern Green Bay, southern Green Bay, and in association with the Muskegon River on the eastern shore. Insofar as can be determined, only relatively small numbers ever existed elsewhere and these populations were greatly reduced by overfishing and destruction of stream spawning habitat by the time the first descriptions of the fisheries were made (Milner 1874; Smith and Snell 1891).

In 1975, all walleye stocks in Lake Michigan were at a very low level of abundance (Fig. 3). Catches in Wisconsin waters of southern Green Bay began a gradual decline in the 1920s (judging from the data of Crowe et al. 1963, the brief recovery in the 1940s was due to immigration from northern Green Bay); and recruitment to the northern Green Bay and eastern stocks began to decline in the mid-1950s. Other changes in Lake Michigan fish stocks included the buildup of rainbow smelt during the 1930s, of sea lamprey about 1950, and of alewife during the 1950s. An extremely large year-class of walleye was produced (not coincidentally?) in northern Green Bay immediately after the rainbow smelt stock sagged in 1943. Reasons for the buildup of the

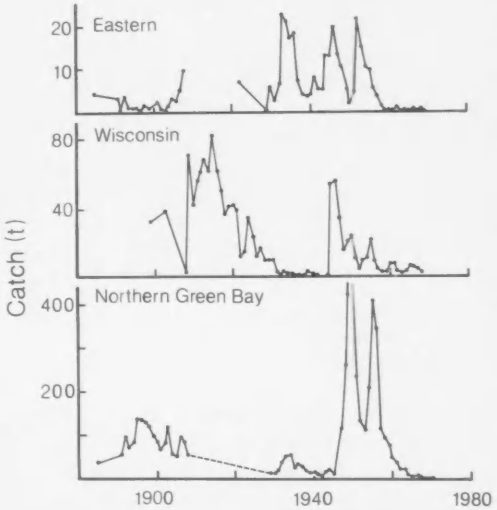

FIG. 3. Commercial catches of walleyes from the eastern, Wisconsin (mostly southern Green Bay), and northern Green Bay waters of Lake Michigan, 1885–1969.

eastern population in this century, and its subsequent oscillations, are not known.

The declines in northern Green Bay and along the eastern shore were most likely due to some effect of alewives on larval walleyes. Tremendous numbers of alewives entered walleye nursery areas in Little Bay de Noc and Muskegon Lake at about the "critical" time. Reductions in yellow perch (*Perca flavescens*) and other species have been attributed to alewife also (Wells and McLain 1973). However, recent plantings of fingerling walleyes in Little Bay de Noc have been successful (J. Peterson personal communication).

Exploitation, sea lamprey predation, and egg viability were of minor importance in the decline of northern Green Bay and eastern shore stocks (W. R. Crowe and the Michigan Department of Natural Resources unpublished data). Adequate numbers of adult walleyes were present in both areas for about 10 yr after recruitment began to fail. For the eastern shore stock, annual fishing mortality was approximately 14–28%. At Bay de Noc, total annual mortality of tagged walleyes during the period of decline was a rather high 65%. Sport and commercial fishing activity was intensive but only 8.4% of the tags were reported under a voluntary return system. We consider it unlikely that many deaths were caused by sea lamprey predation because wounding and scarring rates were less than 3.5% in both walleye stocks. Eggs taken from the remnant adult stocks were successfully hatched and reared (L. Mrozinski and J. Peterson personal communications).

The decline of walleye in southern Green Bay was presumably due mainly to impairment of reproduction by dams and pollution and, to some extent, degradation of the offshore habitat. Only the Menominee River continued to support a small run of walleyes. Gross pollution of the Fox River affected dissolved oxygen levels at least 43 km from its mouth and had a pronounced effect on the benthic community (Howmiller and Beeton 1970). Additional stress may have been imposed by the rainbow smelt. Schneberger (1937) estimated that smelt had become the most abundant species in Green Bay by the mid-1930s. He noted that smelt ate many of the same foods as the native species and that they were piscivorous. The fish population of southern Green Bay is now dominated by carp (*Cyprinus carpio*), smelt, and alewife. Recent plantings of fry and fingerlings have established some walleyes in Sturgeon Bay (L. Kernan personal communication).

Lake Huron

A number of important walleye stocks existed in Lake Huron. The Saginaw Bay population, the second largst in the Great Lakes, supported annual yields occasionally in excess of 700 t. In addition, it probably contributed to fisheries some 90 km to the north in Thunder Bay, Mich. Harvests from Thunder Bay, Georgian Bay, North Channel and the northwestern waters (Statistical District MH-1) sometimes surpassed 50 t. The south end of Lake Huron still has a prominent fishery (discussed in the next section). Some of these stocks declined, but others remained stable despite the buildup of rainbow smelt in the 1930s, sea lamprey in the 1940s, and alewife in the 1950s.

In the mid-1970s, healthy stocks remained in Michigan waters of northwestern Lake Huron, Georgian Bay, and parts of the North Channel (Fig. 4). The main walleye area in northwestern Lake Huron was the lower end of the St. Marys River system; lesser numbers of recruits were supplied by the Cheboygan River. The drop in commercial catch in the early 1900s was due to closure to fishing of the principal spawning area, Lake Munuscong. In Georgian Bay, spawning populations remained in the French, Moon, and Severn rivers, and in the Shawanaga River–Groundhog Island area (Spangler et al. 1977). Fishing pressure has been relatively light on these stocks (with the exception of the Ground-Island stock which is fished commercially) and

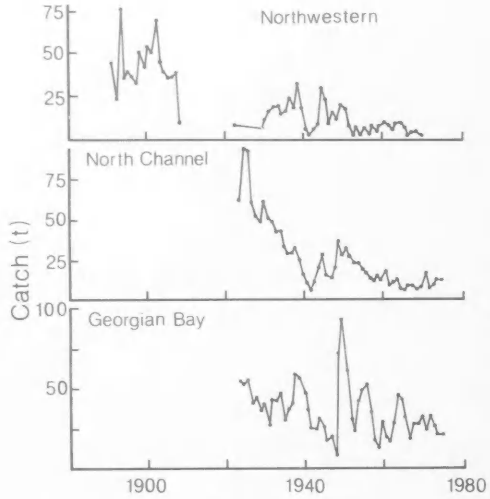

FIG. 4. Commercial catches of walleyes from the northwestern (Statistical District MH-1), North Channel, and Georgian Bay waters of Lake Huron, 1891–1975.

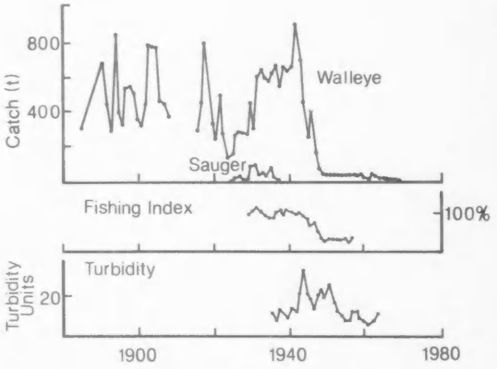

FIG. 5. Commercial catches of walleyes and saugers from Saginaw Bay, Lake Huron, 1885–1969, and trends in the fishing intensity index (Hile and Buettner 1959) and turbidity of the bay (Bay City Water Treatment Plant).

alewives may be less abundant in these areas than in other parts of the lake.

Alteration of spawning habitat was the primary cause for decline among Lake Huron stocks. Gradual declines occurred in these populations: Au Sable River, Mich. — late 1800s; Thunder Bay River — 1920s; and (Fig. 4) North Channel — 1930s. An abrupt decline occurred in the Saginaw Bay stock in the 1940s (Fig. 5). Few of the walleyes spawning in the Au Sable River survived the logging and lumbering era, the run in the Thunder Bay River and the Spanish River (North Channel) probably succumbed to industrial pollutants, and the recent loss of recruitment in the MacGregor Bay stock (North Channel) may have been caused by airborne acids (Spangler et al. 1977).

Saginaw Bay was subjected to increasing amounts of silt, nutrients, and industrial pollutants as the watershed was developed by man. An abrupt change in sauger (*Stizostedion canadense*) catches was the first clear indication of changes in the fish stocks (Fig. 5). Loss of walleye recruitment, beginning in 1944, was associated with increased turbidity (Fig. 5). Presumably, the substratum became unfit for the incubation of walleye eggs (U.S. Fish and Wildlife Service 1969). It should be noted that Bay water was used to incubate walleye eggs in the Bay City Hatchery until the hatchery closed in 1944. Actually, loss of reproductive potential began in the last century with the deterioration of spawning runs into the Saginaw River and other tributaries. The offshore spawning areas, located mainly off the mouth of the Saginaw River and in the part of the bay with the most severe water quality problems, were able to compensate until the 1940s.

Loss of recruitment was reflected in the size and age distribution of the Saginaw Bay population in the 1940s and 1950s (Great Lakes Fishery Laboratory unpublished data). A shift towards larger walleyes indicated that sea lamprey predation and commercial exploitation (which select larger fish) were not critically high; however, as the adult stocks declined, the fishery became relatively more intense. By 1950, catch had dropped by a factor of 33 but effort by only a factor of 3 (Fig. 5). Plantings of 50 million walleye fry in 1972 and again in 1973 met with poor success in the face of large numbers of rainbow smelt and alewives.

Southern Lake Huron, Lake St. Clair, and Connecting Waters

The walleye stocks of southern Lake Huron, the St. Clair River, and Lake St. Clair intermingled. Tagging studies indicated that many walleyes spawning in the Thames River, a tributary of Lake St. Clair, later moved up the St. Clair River to Lake Huron, and in addition there was interchange between these areas and the Detroit River and western Lake Erie (Ferguson and Derksen 1971; Wolfert 1963). Descriptions of the early fisheries substantiated the existence of spawning migrations in the Detroit River (presumably up from Lake Erie) and in the St.

Clair River (down from Lake Huron). As a whole, the walleye stocks in this area remained in good health, with the exception of the Detroit River spawning population (and possibly a few others) which were depleted in the last century. The "fishing up" process in this area began in 1829 (First Biennial Report, Michigan State Board of Fish Commissioners).

The St. Clair River–Lake St. Clair walleye stock has always been large and closely linked to the stock in southern Lake Huron. According to Michigan records, after the Lake St. Clair commercial fishery was curtailed in the early 1890s, over 90% of the catch from "Lake St. Clair and connecting waters" (Fig. 6) came from commercial seining and angling on the St. Clair River. We consider that this fishery exploited a discrete walleye population, spawning in the St. Clair River itself, in addition to walleyes returning from spawning grounds in the Thames River and possibly elsewhere. Michigan and Ontario hatcheries obtained walleye eggs in the 1880s and 1890s from commercial seiners operating along the length of the St. Clair River. The Eleventh Biennial Report of the Michigan State Board of Fish Commissioners clearly records that the run always began in May; this is decidedly different from the March–April run in the Thames River (Johnston 1977). The drop in catch from this stock in the early 1900s was due to curtailment of commercial fishing in Michigan waters. The Ontario fishery was stable until the 1960s, when effort and, seemingly, walleye abundance increased (Fig. 6 and Johnston 1977). In 1970 the fishery was closed because of mercury contamination. Johnston (1977) noted that the apparent increase in walleyes coincided with the extinction of the sauger.

The walleye stock of southern Lake Huron sustained a lake fishery as high as 227 t/yr in addition to the St. Clair River fishery (Fig. 6). The lake fishery was concentrated at the lower end of the basin, principally in Ontario waters. The walleye stock fluctuated strongly in the earliest years of record, perhaps reflecting the dependence of an intensive fishery on strong year-classes. The population has been practically stable since 1905 except for a marked increase in the mid-1930s. Rainbow smelt were not seen there until 1932 (Van Oosten 1937) but possibly they were numerous enough to stimulate the spurt by the walleye population. The subsequent fluctuations in numbers of smelt, alewives, and sea lampreys which took place in Lake Huron had no obvious impact on this walleye stock, possibly because the St. Clair River system acts as a spawning refuge. In 1970, commercial fishing for walleye was banned in Michigan, and in Ontario suspended because of mercury contamination.

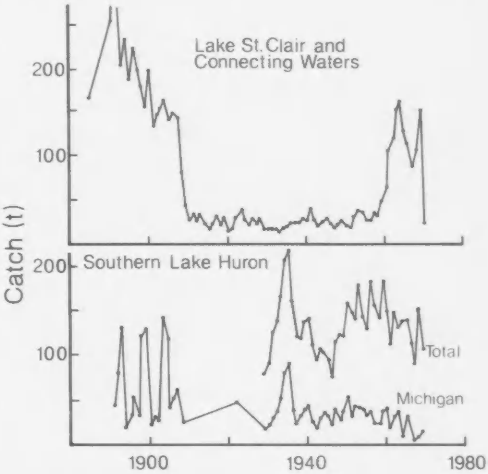

FIG. 6. Commercial catches of walleyes from southern Lake Huron and Lake St. Clair and connecting waters, 1885–1969.

Lake Erie

There were at least two discrete populations of walleyes in Lake Erie, an extremely large one occupying the western and central basins and a small one in the eastern basin. The catch from the western population built to a peak of 7,000 t in the 1950s, then fell precipitously until the fishery was closed in 1970 (Fig. 7). The stock is recovering now. The catch from the eastern population (concentrated in New York waters) was stable until the 1950s, when it increased to a higher level. Both stocks were affected by the rise of the rainbow smelt population in the 1950s,

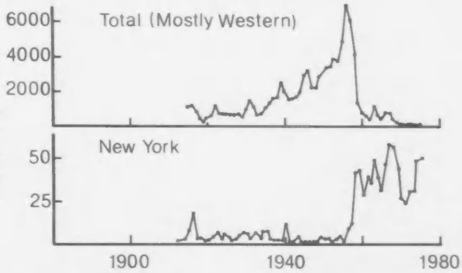

FIG. 7. Commercial catches of walleyes from the New York waters of Lake Erie (eastern stock) and from the entire lake (mostly the western stock), 1913–75.

but alewife and sea lamprey have been too sparse to affect walleyes.

A preponderance of weak year classes since 1954, plus intensive removal of immature and adult fish, led to the decline of the western walleye population (Parsons 1970, 1972; Busch et al. 1975). Indirectly, poor walleye recruitment is attributed to a combination of perturbations (Regier et al. 1969; Hartman 1973; Leach and Nepszy 1976): (1) increased exploitation in Canadian waters, causing a decrease in reproductive potential; (2) increased eutrophication, resulting in loss of habitat and a valuable food organism, *Hexagenia* sp.; and (3) the development of a very large population of rainbow smelt in the central basin. Recruitment of both the walleye in the western basin and also the blue pike (*Stizostedion vitreum glaucum*) in the central and eastern basins became irregular after rainbow smelt became very abundant. The blue pike now appears to be extinct. There is no evidence that smelt affected either species directly, but their habit of eating other fish and the food of other fish (zooplankton) was established (Price 1963). Now that the walleye brood stock has built up through a moratorium on commercial fishing, the effect of smelt on recruitment may have diminished in importance.

Western Lake Erie and its tributaries once contained many prime spawning and nursery areas for walleyes. However, pollution, sedimentation, and damming gradually destroyed or damaged spawning grounds in the Detroit, Huron, Maumee, Sandusky, Cuyahoga, and Grand rivers, and also a number of shoreline breeding sites (Langlois 1945; Busch et al. 1975; Regier et al. 1969). The remaining spawning grounds, principally on island reefs, were sometimes adequate, as evidenced by the maintenance of a large walleye population after many ancestral breeding sites were lost. However, as Regier et al. (1969) pointed out, recruitment should become more variable because a poor hatch at one spawning ground may not be offset by good hatches at other localities. From 1960 to 1970, walleye recruitment was linked to weather conditions on the island reefs (Busch et al. 1975). Steadily rising temperatures and few storms during the incubation and posthatching period favor the formation of large year-classes. However, the poor recruitment of walleye during the critical years of 1955–61 is not likely to be explained as a chance occurrence of temperatures unfavorable to incubation of eggs and survival of fry. In four of those years (1955, 1958–60) average April–May air temperatures at Monroe, Michigan, were 2.0 to 6.7 deg. C above normal.

The increase in walleye catches from New York waters of the eastern basin in the 1950s seemed to represent a real increase in the available stock because total fishing effort was nearly constant (although possibly redirected). The increase may have been a reaction to reduced competition from blue pike or to increased forage provided by rainbow smelt. Walleye recruitment was stable there (until the last few years) despite a large population of smelt. Possibly smelt did not concentrate near the walleye spawning reefs, which are thought to be located off the New York shore.

Lake Ontario

The walleye was always confined to the shallower, eastern end of Lake Ontario. The largest walleye stock, spawning in the Bay of Quinte and then moving out along the Ontario shore, declined in the 1960s; the population in New York waters began a gradual decline in the 1920s (Fig. 8). Minor spawning populations were eliminated by overfishing or loss of habitat in the last century.

Lake Ontario was the first of the Great Lakes to be invaded by marine fish. Sea lamprey and alewife, abundant for over 100 yr, and rainbow smelt, abundant since the 1940s, have had no known negative effect on walleyes. On the contrary, alewife and smelt became important foods (Smith 1892; Payne 1963), and the increased catches of walleyes in Ontario waters during the 1950s may have been partially due to the new smelt forage. However, another invader, the white perch (*Morone americana*), probably caused the decline of walleye recruitment in the Bay of Quinte beginning in 1960 (Christie 1973). Declining water quality may have been a factor also. The reason for the collapse of the stock in New York waters is not at all clear. Climatic changes,

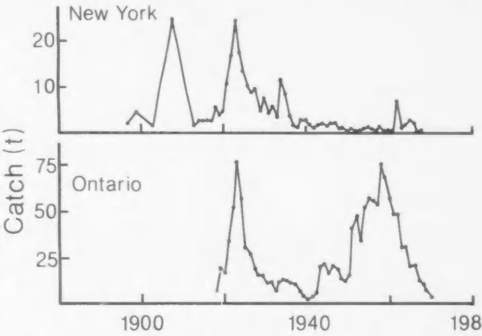

FIG. 8. Commercial catches of walleyes from the New York and Ontario waters of Lake Ontario, 1897–1970.

overfishing, and loss of spawning habitat are the most likely explanations. Only the St. Lawrence River spawning stocks have survived (W. Pearce personal communication).

General Discussion

In Table 1 we summarize the sources of stress affecting specific walleye stocks (including many spawning populations). The dates of major decline shown are subjective estimates for those stocks which declined gradually; for other stocks, more exact dates were assigned on the basis of either year-class strength or an abrupt decrease in walleye abundance. Our judgments as to which sources of stress were of major or minor importance in the decline of stocks were largely based on circumstantial evidence. Though each stock had unique characteristics and problems, there were some similarities.

Of the 21 walleye stocks, relatively stable ones persisted in only five areas: Lake Superior (Wisconsin), Lake St. Clair–southern Lake Huron, eastern Lake Erie, northwestern Lake Huron, and Georgian Bay — and the future of the first three is uncertain. All of the stable stocks seem to have been exploited relatively lightly, especially over the past few decades and, perhaps, were better able to withstand stresses added by new species of fishes. Sea lamprey, smelt, and alewife abundance ranged from low to high within the areas occupied by these stocks; pollution problems were relatively minor.

Among the walleye stocks which declined, many relatively small spawning populations were damaged during the last century, presumably because of overfishing, destruction of spawning habitat by logging or pollution, or obstruction of spawning migrations by dams. That certain runs were able to survive this era seems miraculous.

Five walleye stocks declined in the first three decades of this century. Populations in Lake Superior, southern Green Bay, the Thunder Bay River, the North Channel, and the New York waters of Lake Ontario declined gradually, as though their habitats were slowly degrading. Causes for their declines could not be confidently asserted, but for southern Green Bay and Thunder Bay there was evidence of pollution, and for Lake Superior we speculated that there may have been a gradual change in environment. Degradation of spawning grounds was a possibility in the other areas too. Overexploitation was suspect (largely by default) in two areas but it could not be substantiated by data on fishing effort. For the stocks in southern Green Bay, the North Channel, and the Thunder Bay River there was some association between the decline of walleyes and the rise of rainbow smelt.

The remaining discussion focuses mainly on the seven walleye stocks which fell abruptly in the last three decades, the period when the fish composition of the Great Lakes was greatly altered. By contrast, walleye populations in inland lakes within the Great Lakes region were practically stable in this period, suggesting that the cause or causes of instability were restricted to the Great Lakes. For each stock the decline can be traced to a series of weak year-classes. Stresses came from moderate to intensive exploitation, water quality problems ranging from light to severe, and varying degrees of interaction with exotic fishes which, if they played no important part in the decline, may be suppressing recovery. Only one stock (western Lake Erie) has recovered, and it was favored by the relatively low density of smelt and alewife in the nursery areas.

Listed in approximate order according to the date that recruitment began to fail, these stocks are: Saginaw Bay (1944), northern Green Bay (1953), eastern Lake Michigan (mid-1950s), western Lake Erie (1955), Nipigon Bay (late 1950s), Bay of Quinte (1960), and Black Bay (mid-1960s). We note that the 1950s was an especially disastrous period. There was only a hint of a sequential pattern beginning in Lake Michigan in the mid-1950s (if we acknowledge that pollution was the problem in Saginaw Bay) and ending at Lake Ontario and Lake Superior in the 1960s. The only exotic fish with a similar dispersal pattern and common to all areas is the rainbow smelt. However, we are confident that the smelt was not entirely responsible for the collapse of all of these stocks.

The smelt has had an effect on the walleye that was both positive and, probably, also negative. Many walleye fisheries (Saginaw Bay, eastern Lake Michigan, southern Lake Huron, western and eastern Lake Erie, Bay of Quinte, and Black Bay) increased while smelt were becoming established. In Saginaw Bay the smelt forage probably improved walleye growth, but in western Lake Erie, growth was constant and recruitment increased (Hile 1954; Regier et al. 1969). The importance of smelt in the diet of walleyes was established in western Lake Erie, Bay of Quinte, the North Channel, Georgian Bay, and northern Green Bay (Price 1963; Payne 1963; Spangler et al. 1977; Wagner 1972).

Evidence for negative effects of smelt on walleye is purely circumstantial. Poor walleye recruitment in Green Bay, western Lake Erie, and elsewhere was associated generally with high

TABLE 1. Summary of stresses affecting walleye stocks in the Great Lakes and approximate dates of major declines.

		Source of stress[a]								
					Alteration of spawning habitat		Alien species			
Stock	Date of major decline	Exploitation	Nutrient loading	Toxic materials	Sedimentation	Restructuring	Smelt	Sea lamprey	Alewife	White perch
Lake Superior										
Michigan	Gradual, 1900s	XX?	—	—	—	—	(P)	(P)	—	—
Wisconsin	None	—	—	—	—	—	P	P	—	—
Minnesota	Late 1800s	XX	(P)	(P)	(P)	—	(P)	(P)	—	—
Black Bay	Mid 1960s	XX	—	—	—	—	P	P	—	—
Nipigon Bay	Late 1950s	X?	—	XX	—	—	P	P	—	—
Lake Michigan										
Eastern	Mid 1950s	P	P	P	—	—	P	P	XX	—
S. Green Bay	Gradual, 1920s	X	X	P	XX	XX	X	(P)	(P)	—
N. Green Bay	1953	X	P	—	—	—	X	P	XX	—
Lake Huron										
Saginaw Bay	1944	X	XX	P	XX	P	(P)	P	X	—
Au Sable	Late 1800s	P	—	—	XX	X	(P)	(P)	(P)	—
Thunder Bay	Gradual, 1920s	P	—	—	XX	X	P	(P)	(P)	—
Northwestern	None	P	—	P	P	P	P	P	P	—
North Channel	Gradual, 1930s	P	—	X	X	P	P	P	P	—
Georgian Bay	None	P	—	—	—	—	P	P	P	—
St. Clair Area										
Detroit R.	Mid 1800s	XX?	P	(P)	P	P	—	—	—	—
L. St. Clair	None	P	P	P	P	—	P	—	P	—
St. Clair R.– S. Lake Huron	None	P	—	P	—	—	P	P	P	—
Lake Erie										
Western	1955	XX	XX	P	X	X	X	P	P	P
Eastern	None	P	P	?	—	—	P	P	P	P
Lake Ontario										
New York	Gradual, 1920s	XX?	P	?	X?	?	(P)	P	P	(P)
Ontario	1960s	P	X	?	P	—	P	P	P	XX

[a] XX = major factor in the decline; X = minor factor in the decline; P = present; ( ) indicate stresses not important in the decline but possibly important in preventing recovery of the stock.

smelt abundance and, conversely, a strong year-class was produced in the upper Great Lakes when smelt abundance fell sharply in 1943. Smelt are voracious and they may have a severe effect on fish communities in which they are not native and which are being stressed in other ways. A seemingly small effect of individual smelt on pelagic larval walleyes, or their food, would be magnified greatly at the population level because of their high density.

The same arguments apply to the alewife. They are piscivorous at times, reportedly eating their own young and those of yellow perch (Sibley and Rinsky-Korsakoff 1931; Rhodes et al. 1974). In southern Lake Michigan, larval alewives made up as much as 76% of the food of adult alewives in September (Rhodes et al. 1974). Since alewife larvae up to 32 mm long have been found in alewife stomachs, they are capable of eating walleyes, which hatch at only 8 mm. It is more likely that alewives compete with plankton-feeding fishes, including young walleyes. In addition, they restructure the plankton community (Wells 1970). Evidence that the alewife has had an effect on many species in the Great Lakes was presented by Smith (1970). In Lake Michigan, the superabundance of alewives was the most likely explanation for the loss of walleye recruitment. On the other hand, we are unable to explain why alewives had no obvious effect on the walleye populations in Lake Ontario. There, as elsewhere, the alewife became an important food item for walleyes.

The sea lamprey has had a severe effect on many Great Lakes fishes but we doubt that it played a significant role in the decline of the Great Lakes walleye. Scarring and wounding rates were very low — less than 3.5% in the four populations for which we have reliable data — and we doubt that many walleyes died "on contact." Laboratory studies by Farmer and Beamish (1973) indicated that the walleye is very low on the lamprey's preference list. Therefore we reason that the lamprey would not attack the walleye much until preferred species became sparse, and that it would select large walleyes over small ones. Data for the Muskegon River run substantiate this (Schneider and Leach 1977). Furthermore, the recent collapses of walleye populations were primarily due to poor recruitment, not poor survival of adults. Also, in Oneida Lake, New York, the walleye and sea lamprey have coexisted for many years. The Oneida Lake walleye population is very dense and its natural mortality rate is among the lowest reported (Forney 1967).

The white perch is the latest exotic fish to invade the Great Lakes and it has already been implicated in the collapse of one walleye stock (Bay of Quinte). We foresee further adverse effects if this species continues to spread throughout the Great Lakes (Busch et al. 1977).

The sauger, now at extremely low levels in the Great Lakes, was a sensitive indicator of water quality changes in western Lake Erie and Saginaw Bay. Both of these sauger stocks plummeted before those of the walleye. In Black Bay, which has no recognized pollution problem, the sauger declined at the same time as the walleye. We wonder if the recent disappearance of saugers from Lake St. Clair, followed by the abrupt increase in walleyes, is a harbinger of things to come.

Exploitation played a major role in the decline of certain walleye stocks in the last several decades when it was combined with other perturbations, such as pollution and exotic fishes. Intensive exploitation reduces the reproductive potential of the population and increases its dependency on stable recruitment. In western Lake Erie the walleye population barely recovered from seven weak year-classes in a row. Other populations (northern Green Bay, eastern Lake Michigan, and Saginaw Bay) seemingly had adequate spawning stock for a decade after the decline began yet were unable to produce a large year-class. It is difficult to judge how large a brood stock should be protected from the fishery and for how long, because the effects of weather on recruitment tend to obscure the relation between stock and recruitment.

Indirectly, those factors which increase walleye growth, such as eutrophication or a new forage species such as smelt or alewife, increase the effect of the fishery on walleye recruitment. As growth increases, a fishery will take more walleyes before they mature. This surely occurred in western Lake Erie and Saginaw Bay. In Lake Erie (Fig. 9), a fishery selective for walleyes larger than 394 mm (the highest size limit actually imposed), for example, would have taken no immature females in the period when growth was normal (e.g. in 1927–28, a total length of 180 mm was reached in two growing seasons — Deason 1933); but all the females in the catch may have been immature in the later period, when (1) growth was fast (e.g. in 1960, a total length of 368 mm was reached in two growing seasons — Parsons 1970) and (2) exploitation was intensive. A similar shift in the size-maturity relationship occurred at Saginaw Bay, but there the shift was not as marked because the increase in growth was less (Hile 1954). The proper man-

TABLE 2. Commercial catches of percids from the Great Lakes in 1975 as compared with those in peak years (modern era).

Lake	Species	Peak			1975		Reduction in catch (%)
		Year	Catch (t)	% of total catch	Catch (t)	% of total catch	
Ontario	Walleye	1958	76	7	2	<1	97
	Blue pike	1952	294	22	0	0	100
	Yellow perch	1970	455	31	299	22	34
Erie	Walleye	1956	6,988	20	114	<1	98
	Blue pike	1949	10,787	45	0	0	100
	Yellow perch	1969	15,044	56	4,593	26	69
Huron	Walleye	1942	1,071	18	126	5	88
	Yellow perch	1966	703	23	368	16	48
Michigan	Walleye	1950	612	5	2	<1	99
	Yellow perch	1964	2,647	22	360	2	86
Superior	Walleye	1966	171	4	1	1	99

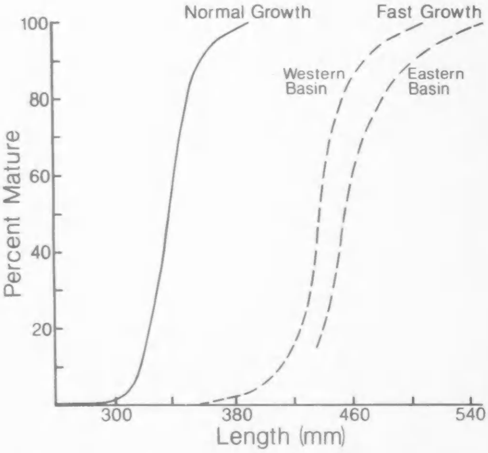

FIG. 9. Relations between length and percent mature for female walleyes in Lake Erie under conditions of normal (1927–33 data from Deason 1933) and fast (1964–66 data from Wolfert 1969) growth.

agement strategy in both fisheries would have been to increase the minimum size limit or reduce the harvest.

The depressed condition of the percid fisheries in each of the Great Lakes in 1975, as compared with peak years, is clearly evident from the statistics in Table 2. The commercial catch of walleye was down from 88 to 100%, of yellow perch from 34 to 100%, and of blue pike by 100% (apparently extinct). These data faithfully reflect the present low abundance of percids with the exception of those areas (such as western Lake Erie) where fisheries were curtailed to protect the remaining stocks. Conservative management policies will be needed to preserve the remaining stocks in the unstable Great Lakes environment, pollution must be reduced to restore habitats, and special management techniques will be needed to reestablish spawning populations of walleyes already lost because the homing tendency of walleyes hinders recolonization through natural dispersal.

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Biology of the Percids

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The structure, origin, and spread of the family Percidae are reviewed briefly, and its characteristics compared with those of other families of freshwater fishes. It is suggested that the percids, essentially riverine, have been restricted in their success in North America by the presence of the Centrachidae. Percids are defined as temperate mesothermal fish, and this physiological characteristic together with osmoregulatory capacity and swimming performance is shown to limit the ranges of the perches. The degree of development of the tapetum lucidum in *Stizostedion* spp. and of the lateral line in all percids is related to differences in pattern of development, feeding behavior, and habitat. Reproductive, feeding and migratory behaviour are also reviewed.

Key words: Percidae, structure, origin, biology, morphology, systematics, migration

COLLETTE, B. B., M. A. ALI, K. E. F. HOKANSON, M. NAGIĘĆ, S. A. SMIRNOV, J. E. THORPE, A. H. WEATHERLEY, AND J. WILLEMSEN. 1977. Biology of the percids. J. Fish. Res. Board Can. 34: 1890–1899.

Les auteurs passent brièvement en revue la structure, l'origine et l'étendue de la famille des Percidae et comparent ses caractéristiques avec celles d'autres familles de poissons d'eau douce.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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Ils suggèrent que les percidés, essentiellement fluviatiles, ont vu leur succès entravé en Amérique du Nord par la présence des Centrarchidae. Les percidés sont définis comme poissons mésothermes tempérés, et on démontre que cette caractéristique physiologique, couplée à une capacité osmorégulatrice et à une performance de nage, limite les aires des perches. Le degré de développement du tapis réflecteur chez *Stizostedion* spp. et de la ligne latérale chez tous les percidés est lié à des différences dans le développement, le comportement alimentaire et l'habitat. Les auteurs passent également en revue le comportement reproducteur, alimentaire et migratoire.

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This paper reviews important morphological characters of the family and summarizes available information on the biological processes of reproduction, feeding, and migration. An attempt is made to provide a general overview of the family and then to concentrate on the species of most interest to PERCIS — members of the genera *Stizostedion*, *Perca*, and *Gymnocephalus*.

Composition and origin of the Percidae — The Percidae, with about 163 species, is a basal percoid freshwater fish family that resembles the Centrarchidae and the Cichlidae and differs from the Serranidae and Percichthyidae and many other familes of marine percoids in the absence of a subocular shelf and in having one or two instead of three anal spines. The Percidae differs from most other percoid families in having one or no predorsal bones instead of two or more. The anatomical characteristics of the family are summarized by Collette and Bănărescu (1977). The family is divisible into two subfamilies (Collette and Bănărescu 1977): the Percinae, which have large anal spines and a well-developed anteriormost interhemal bone, and the Luciopercinae, which have the anal spines poorly developed and the interhemal bones of uniformly small size. In each subfamily parallel evolution has led to mostly small, benthic, rheophilic forms with terete or depressed bodies and reduced or vestigial swimbladders. This differentiation is reflected by recognition of two tribes in each subfamily. Within the Percinae, the Etheostomatini (the three genera of North America darters) are interpreted as derivatives of the Percini (*Perca, Gymnocephalus,* and *Percarina*). Within the Luciopercinae, the Romanichthyini (the European *Zingel* and *Romanichthys*) have evolved from the Luciopercini (*Stizostedion*).

The Percidae appears to have originated from some anadromous basal percoid family during the Cenozoic in Europe, spreading to North America through at least two separate invasions. A critical review of available fossil material (*Amphiperca, Anthracoperca, Leobergia, Plectropoma, Propercarina*) is needed not only to provide information on paths and times of movements but also to help interpret evolutionary trends within the family.

Evolutionary characteristics of Percidae and other freshwater fishes — Before proceeding with the morphology and biology of the percids, we consider briefly some phylogenetic and historical factors that have influenced the distribution and evolution of primary freshwater fishes. We follow Myers' (1938) definition of primary freshwater fishes as those groups of fishes restricted to freshwater and whose evolution has taken place in freshwater. Of the approximately 21,000 species of living fishes (Cohen 1970), an astonishingly high 41.2% live in freshwaters, which constitute only about 0.0093% of the total water area of the world (Horn 1972). Most freshwater fishes are relatively primitive, soft-rayed (malacopterygian grade) fishes that differ from more advanced, spiny-rayed (acanthopterygian grade) fishes in a series of characters including the following seven, which are of evolutionary importance:

Character	Malacopterygii	Acanthopterygii
1. fin rays	soft rays	some true spines
2. scales	cycloid	ctenoid
3. pelvic fin position	abdominal	thoracic (or jugular)
4. pelvic fin rays	more than 5	1 spine and 5 rays
5. maxilla	included in gape	excluded from gape
6. swimbladder	physostomous (connected to gut)	physoclistous (not connected to gut)
7. dorsal fins	1 (sometimes followed by adipose fin)	2 (sometimes joined)

These evolutionary advances confer selective advantages on the acanthopterygian fishes in manoeuvrability (1, 3, and 7), protection against predators (1, 2, and 4), maintenance of contact between the sexes in spawning (2), more efficient feeding (5), and the ability to colonize relatively deep waters (6).

The largest component of primary freshwater fishes is the superorder Ostariophysi, which includes about 6000 species (catfishes, minnows, loaches, characins, and their relatives). They have two important adaptations that have aided them in retaining dominance over the freshwaters of the five major continents: the Weberian apparatus, a chain of small bones that links the inner ear with the swimbladder thereby increasing their hearing ability and an alarm substance (Schreckstoff) that warns other members of their species when an individual is wounded by a predator (Pfeiffer 1967; Rosen and Greenwood 1970; Roberts 1973). Many ostariophysans have a low oxygen demand and a high tolerance of elevated CO_2 concentrations.

Although spiny-rayed (acanthopterygian) fishes dominate many marine areas such as coral reefs, several families have successfully invaded freshwater. The three most successful freshwater percoid families are the Cichlidae (South America and Africa), Centrarchidae (eastern North America), and Percidae (temperate waters of the northern hemisphere). The Centrarchidae and Cichlidae are primarily laterally compressed fishes adapted for life in lakes. The Percidae, however, lack specific adaptations to lacustrine life and appear to have diverged less from their anadromous ancestors. Kitchell et al. (1977) discuss the riverine nature of percids at greater length. Presence of the Centrarchidae in eastern North America may have been a factor in limiting the number of large percids to three, the yellow perch (*Perca flavescens*), the walleye (*Stizostedion vitreum*), and the sauger (*S. canadense*). Five comparable species, the perches *P. fluviatilis* and *P. schrenki* and the pikeperches *S. lucioperca*, *S. volgense*, and *S. marinum* occur in Europe, where the absence of the Centrarchidae may have been a factor that permitted their evolution and that of the four moderate-sized percids of the genus *Gymnocephalus*.

Limits to ranges — Ranges of percids are limited by three main factors. Two are common to all primary freshwater fishes — highlands physically separating the upper parts of different river systems, and salt water physiologically preventing movements from the lower part of one river system to the next. In addition, percids are limited by high summer temperatures. They are adapted to temperate climates of the northern hemisphere where temperatures range from <4°C for more than 8 mo in northernmost latitudes to about 32°C in southernmost extremeties of their native range. Physiological optima vary from 22 to 28°C and ultimate upper incipient lethal temperatures from 29 to 35°C for those species that have been tested (Hokanson 1977).

The best data available on the thermal and salinity limits to percid distribution are for natural and introduced populations of *P. fluviatilis* and *P. flavescens*. Evidence from introductions of *P. fluviatilis* to Australia has been used to develop concepts concerning factors limiting the range of this species and of *P. flavescens* in their respective ranges in Eurasia and North America (Weatherley 1963, 1974, 1977; Weatherley and Lake 1967).

Thermal preferenda for these two percid species, and others also, compared with their upper lethal temperatures, suggest that in many parts of their ranges they would avoid dangerously high temperatures when possible (Hokanson 1977). High winter temperatures may also retard maturation and damage oocyte formation in *Perca* spp. (Weatherley and Lake 1967; Hokanson 1977). However, near the edges of their ranges at certain points, especially in Italy, central USA, and Australia, high temperature may act fairly directly to limit range extension (Weatherley 1963, 1977; Hokanson 1977). Willemsen (1977) reported a somewhat higher lethal temperature (33.5°C) for *P. fluviatilis* than others have found and McCormick (1976) has found a similar upper lethal temperature in *P. flavescens*.

Perch can tolerate salinity of up to 10‰ (Driver and Garside 1966; Privolnev 1964). As Thorpe (1977a) noted, this enables them to survive in the Baltic and Aral seas, and Chesapeake Bay, but it also means that they are unable to extend their present range by sea coastal movements to new river mouths (Weatherley 1974, 1977). Other species of percids (except *S. marinum* and *Percarina demidoffi*) have been less salinity tolerance and so are restricted to strictly freshwater.

Morphology

Swimbladder — The swimbladder is an important structure that enables many species of bony fishes to be neutrally buoyant, thereby allowing them to rest motionless in midwater. Members of the two most primitive tribes of the Percidae, the Percini and Luciopercini, are moderate- to large-sized species with well-developed swimbladders. Swimbladders are reduced (*Percina*) or absent in the Etheostomatini (Morgan 1936) and Romanichthyini, an adaptation common to benthic fast-stream inhabitants.

Lateralis system — Percids have a relatively well-developed lateralis system, although it is reduced on the head and body in some Etheostomatini. The canals on the head lie in grooves in the underlying cranial bones. The size and shapes of the neuromasts vary from species to species (Jakubowski 1967). Species of Luciopercinae have two supplementary lateral lines on each side of the tail (absent in the specialized genus *Romanichthys*), whereas species of Percinae either have no lateral line on the tail or else the main lateral line extends out onto the tail for a short distance. *Percina*, the most primitive genus of the Etheostomatini, has a system of uninterrupted head canals and a lateral line extending from the edge of the opercle to the hypural plate and out onto one or more scales of the caudal fin in several subgenera (Page 1977). *Ammocrypta* is similar to *Percina* but shows a reduction in some species in the number of pores in the preoperculomandibular canal from 10 to 8 or 9. There are many reductive modifications of the lateralis system within the advanced and speciose genus *Etheostoma*, as Page (1977) showed in his survey of the lateralis system of darters. Pores have been lost and canals have become interrupted in each of the four main parts of the lateralis system — body lateral line, supratemporal canal, infraorbital canal, and preoperculomandibular canal — especially in the most highly advanced subgenera such as *Hololepis* and *Microperca*, which are inhabitants of still waters.

Percids are divisible into two groups based on lateral-line structure and biology (Jakubowski 1963, 1966, 1967; Disler and Smirnov 1977; Page 1977): (1) Active pelagic predators (*Perca* and *Stizostedion*) and rheophilous benthophages (*Zingel*, *Romanichthys*, and Etheostomatini) — sight feeders with moderately developed lateral line; cephalic canals mostly enclosed in bone. (2) Benthophage dwellers of slow-flowing waters — cavernous lateral line (*Gymnocephalus* and *Percarina*); head canals strongly expanded with only narrow bony bridges over the neuromasts.

Ruffe (*Gymnocephalus cernuus*) hatch at a less-developed stage than perch and take about 7 days to reach the same level of development as newly hatched perch. Lateral-line canals are much larger in juvenile ruffe than in juvenile perch and contain more large sense organs. The external walls of ruffe head canals are membranous, providing a high directional sensitivity. Ruffe fry can feed at night, in the dark, using the lateral-line system. The neuromasts in the canals seem to be most sensitive to vibrations of low intensity, while those on the surface of the body (pit organs) are sensitive to more intense vibrations, thus acting as a defense system against predators.

Visual apparatus — Percids occupy a wide depth range from streams only a few centimetres deep (North American Etheostomatini) to a depth of at least 27 m for *Stizostedion vitreum vitreum* (Regier et al. 1969) and 56 m for *Perca flavescens* (Thorpe 1977b). Thus, percids are exposed to a wide variety of light intensities. Many of the shallow-living darters have pigment on the upper surfaces of their eyes that may serve as protection against the glare of the sun. Curd (1966) studied the retinal structure in 26 species of darters and found that darter retinae are generally modified for acute photopic vision. Retinae in darters are basically similar but do show some variations that are more closely associated with feeding habits than habitat. No detailed studies appear to have been published on the structure of the eyes of species of Romanichthyini.

Comparison of morphological structure and electrophysiological responses showed that the eyes of the two North American species of *Stizostedion* were similar except for the retinal epithelial pigment (REP) (Ali and Anctil 1968). Adult walleye from Ontario waters had more REP and less reflecting material than adult sauger from the same area, correlated with differences in habitat and behavior between these two species. Both species are adapted for feeding at low light intensities, the sauger particularly so. Wunder (1930) observed a correlation between the turbid nature of Balaton Lake, Hungary, and the occurrence of a reflecting layer in the eyes of *S. lucioperca*, *S. volgense*, and *G. cernuus* and Moore (1944) found the same for the walleye (*S. vitreum vitreum*). More recently, on the basis of a histological study of cone types and mosaics, Ahlbert (1970) suggested that though the Eurasian perch and pikeperch are both piscivorous, cone arrangement in the former is more adapted for movement detection, while the latter is better equipped for greater sensitivity as the bottom-dwelling ruffe is.

The reflecting material of the tapeta lucida in *Stizostedion* is a reduced pteridine, 7,8-dihydroxanthopterin, in the epithelial processes. It occurs as densely packed anisometric granules of about 0.5 mm long (Zyznar and Ali 1975). The tapetum lucidum in the sauger is not only more developed but is also more uniformly developed within the eye, whereas in the walleye it is well-developed only in the ventral region. Other structural differences suggest greater light sensitivity in the sauger. In both species, photomechanical responses to light and dark are restricted to the masking pigment (REP) and the rods. The cones are immobile (Ali and Anctil 1977). Electroretinographic determination of flicker fusion frequencies (FFF) showed that whereas in the light-adapted state there is no difference between the walleye and sauger, in the dark-adapted state maximum values are attained at a lower light intensity in the sauger (Ali and Anctil 1977). This may be related to the greater development of the tapetum in the sauger and the consequent increase in reflectivity within its eye in comparison with the walleye.

The cones of *Stizostedion* contain multiple droplets of mitochondrial origin as in the killifish (Anctil and Ali 1976). They appear to act as light guides or funnels (Ali et al. 1977) for focusing light on the rods in the dark-adapted state. In this state, the rods are in groups optically isolated from each other by the tapetal processes. Light is reflected back and forth between the tapetal processes with additional absorption by the rods after each reflection. The passage of light through the cones and the position of the REP at the level of the cone ellipsoids limit the angle of acceptance of the cones and increase that of the rod groups — increasing sensitivity.

This mechanism is absent in *Perca*. There is no apparent difference between the retinas of *P. flavescens* and *P. fluviatilis* either in structure or in the nature of their visual pigments. In contrast to the immobile cones in *Stizostedion*, the cones in *Perca* are capable of movement (Ali and Wagner 1976) which may be related to the cones being smaller and to the absence of a tapetum lucidum in *Perca*. There is no difference between *Perca* and *Stizostedion* as far as their visual pigments, scotopic as well as photopic, are concerned. In the four species studied, the rods contain pigment based on Vitamin A_2 and maximally absorbing between 530 and 535 μm. The cones, which are either single or double, contain green (single) and red (both of the double) pigments. There are no blue cones. Thus, this genetically fixed factor, viz visual pigments, is the only one common to the four species.

Central nervous system — The external morphology of the brain in fishes of the order Perciformes is extremely varied and there are differences between families, genera, and sometimes between species. Kirka (1963) described and illustrated the brains of the eight species of percids (belonging to all three European tribes) inhabiting the Danube basin. He found that rheophilic species (*Zingel* and *Romanichthys*) have the skull depressed, the brain flattened, and the cranial cavity largely filled with brain tissue. Limnophilic species (*Stizostedion*, *Perca*, and *Gymnocephalus* spp.) have the corpus cerebelli extending vertically above the rest of the brain and the cephalic cavity is not filled by the brain to the same extent as in the rheophilic species. Similar comparative data on the North American Etheostomatini are not available. The ecological significance of gross differences in brain morphology is unknown.

Biology

Reproduction — Percids are adapted to rising temperature conditions in spring and consequently have evolved an intermediate range of developmental times (i.e. compared with temperate stenotherms and eurytherms). Percids are characterized by a long, annual reproductive cycle with gonadal growth in fall and winter that culminates in spawning in spring (Hokanson 1977). Maturation occurs below 12°C and spawning occurs from late February through early July at temperatures from 3 to 26°C. A summer gonadal refractory period ensures an annual reproductive cycle. Gamete maturation, spawning, embryo and larval development, and commencement of independent feeding by larvae each have successively higher thermal requirements. Percids can adjust to different temperature regimens by shifts in their spawning season as shown by introductions into new environments (Aksiray 1961; Weatherley 1963). Spawning time of a given stock is modified only slightly by changes in temperature. Stocks adjust to accelerated thermal regimens by spawning at higher temperatures and to prolonged cold weather by spawning at colder temperatures (Rawson 1957; EIFAC 1968; Priegel 1970; Jones et al. 1977). These shifts in spawning temperature are made at the expense of gamete viability at temperature extremes (Hokanson 1977).

There is a wide variety of reproductive behavior in the Percidae. Many members of the most specialized tribe in each subfamily (Etheostomatini and Romanichthyini) develop epidermal breeding tubercles during the spawning season (Collette 1965), which facilitate maintenance of body contact between spawning pairs, especially important in moving waters where most of these species spawn. Members of the larger-sized, more generalized tribes (Percini and Luciopercini) lack these structures and usually spawn in more slowly moving waters, generally displaying little external sexual dimorphism. Males of most species of darters (Etheostomatini) are much more brightly colored than are females, especially during the spawning season. Fecundity varies from 240 to 2000 eggs averaging 1.00–2.22 mm diam in 13 species of Etheostomatini (Winn 1958a) and from 3000 to 1,185,000 eggs averaging 0.55–1.10 mm diam in the five species of European percids studied by Kryzhanovsky et al. (1953). Filuk (1962) reported the maximum fecundity of *S. lucioperca* as 2,500,000 eggs.

Darters spawn in a variety of habitats, on aquatic vegatation, in gravel, and under stones. Reproductive behavior of representative species of Etheostomatini has been summarized by Winn (1958a, b) and will not be treated further here. Balon et al. (1977) divide the Percidae into seven reproductive guilds and discuss the reproductive styles that have evolved in representatives of each guild.

Perca fluviatilis and *P. flavescens* spawn between February and July in the northern hemisphere and between August and October in the southern. The first females spawn earlier and at a higher temperature the lower the latitude, recorded temperatures ranging from 5 to 14°C (Thorpe 1977a). Other, local factors influence the timing of this event, for example, the occurrence of spring floods which allow perch to utilize the inundation zone of some large rivers for egg deposition. Presumably, natural selection ensures that reproduction occurs when the ensuing larvae can enter an environment with food resources sufficient for the survival of the maximum number, but critical data are lacking on this point. At the time of egg deposition, each spawning female is followed closely by several males, which shed milt close to her vent as the single, convoluted egg-strand is extruded and laced around submerged plants or debris, mostly in water 0.5–3 m deep (Fabricius 1956; Harrington 1947; Hergenrader 1969). Although defence of the eggs by the female has been observed in a tank, it is not known if this occurs regularly in the wild. The relatively unspecialized requirements for spawning substrate allow the perch to use almost all slow-moving or static waters within their geographical range. Fecundity varies strikingly between localities, egg number ranging from 950 to 210,000; egg diameter varies from 1.0 to 2.1 mm (Thorpe 1977a).

Stizostedion lucioperca spawns between late February and July, being earlier in lower latitudes. The thermal threshold for the beginning of pikeperch spawning is about 12°C (Deelder and Willemsen 1964; Muntian and Reznitchenko 1967). Lower temperatures, even down to 5.8°C (Bastl 1969), have been found in reservoirs south or southeast of Poland (Orava Reservoir — northern Slovakia, Volga estuary, Don estuary, Middle Dnieper, Azerbaidjan lakes). On the other hand, Brofeldt (cited by Muntian and Reznitchenko 1967) mentioned 14°C for Finnish lakes. The date of first spawning at any one locality varies between years. Local factors such as water temperature during gonad maturation (Filuk 1962; Hokanson 1977) and atmospheric pressure (Tesch 1959) influence the timing of this event. Males build nests and protect the brood: They may be monogamous. Nests are built at a depth of one to several metres, on hard bottom in the form of flat pits surrounded by a ridge of shells or gravel, generally in turbid waters, although spawning does take place in very clear water. Plant roots are, however, frequently used as substrate (Kryzhanovsky et al. 1953).

Both *S. vitreum vitreum* and *S. canadense* spawn between March and June. Spawning of walleye normally begins shortly after ice breaks up in the lake, at water temperatures of 5.6–11.1°C, and sauger often spawn immediately after the walleye. Walleye spawn at depths of 10 cm to several metres over various types of bottom in streams and lakes where there is sufficient exchange or movement of water to allow for ventilation of eggs. The two species may utilize the same areas of gravel or rubble in turbid lakes or turbid rivers. Both species have simple spawning habits; there are no redds and they broadcast their eggs with no parental care. Walleye frequently spawn in aggregations, whereas sauger and pikeperch spawn in pairs or small groups (Colby et al. 1977).

Gymnocephalus cernuus is an intermittent spawner (Travkina 1971) on a hard bottom of sand, clay, or gravel. The main spawning period lasts from the middle of April till June (Nolte 1939; Fedorova and Vetkasov 1974; Willemsen 1977). The maximum number of eggs may amount to 200,000 per female; the egg diameter is 0.5–1 mm (Johnsen 1965).

Feeding — Larger percids start feeding upon zooplankton and switch within some weeks to insect larvae and larger invertebrates. Darters (Etheostomatini) continue to feed on insect larvae and other invertebrates. The diet of the ruffe (*Gymnocephalus cernuus*) hardly changes during their lifetime: zooplankton, chironomids, oligochaetes and amphipods (Biro 1977; Willemsen 1977). The species of *Perca* and *Stizostedion* become piscivorous after different periods of time. Although piscivorous percids seem to show some preference concerning species or prey size, the wide variety in diets shows that availability of prey is more important than preference. Prey size rarely exceeds half the length of the predator and usually is considerably less. For pikeperch measuring 11–70 cm, the mean prey length amounted to 6–12 cm, whereas perch up to 40 cm consumed prey in mean length not more than 9 cm (Biro 1977; Popova and Sytina 1977; Willemsen 1977).

The diets of yellow perch and Eurasian perch are much alike: both feed on bottom invertebrates (chironomids, amphipods, mysids, etc.) for a rather extended period. The length at which fishes become predominant in the diet of Eurasian perch varies between 10 and 25 cm (Hartmann and Nümann 1977; Holčík 1977; Rundberg 1977; Willemsen 1977; Popova and Sytina 1977). This transition to feeding on fish may result in an increase in growth rate (Thorpe 1977a) but even when feeding mainly upon invertebrates, perch can grow extremely fast (Willemsen 1977).

Walleye prey mainly on yellow perch, and then primarily on the age-0 group, and so may considerably affect the year-class strength of the latter species (Atton and Kallemeyn unpublished data; Forney 1977; Johnson and Hale 1977; Kelso and Ward 1977; Nelson and Walburg 1977; Swenson 1977). Other fish species frequently consumed are smelt, alewife, gizzard and threadfin shad, and black crappie. Insects and crayfish sometimes form an essential part of the diet (Johnston 1977).

Sauger feed upon nearly the same species as walleye, which might lead to food competition, but according to Fitz and Holbrook (unpublished data) in Norris Reservoir that need not occur because these species tend to be concentrated at different depths.

Pikeperch start feeding upon fish at a length of 5–10 cm, depending upon the abundance of zooplankton and on the availability of prey fish (Nagięć 1977), and are then the most obligatory fish-feeding species of percid. Main prey species are cyprinids, coregonids, perch, ruffe, and smelt. In lakes where smelt is abundant, this species is the preferred food (Deelder and Willemsen 1964; Wiktor 1962; Rundberg 1977) but growth rates based upon diets of cyprinids or smelt appear to be virtually the same. After reaching a length of about 50 cm, pikeperch increase the diversity of species in their diet (Nagięć 1977; Rundberg 1977; Willemsen 1977). Although the diets of pikeperch and perch are nearly identical, food competition does not occur if food availability is high (Willemsen 1977).

Cannibalism occurs frequently among percids if food conditions are inadequate, and may then even reach a level where their own kind forms the main food resource, in many cases resulting in self-regulation of the stock (Biro 1977; Chevalier 1973; Forney 1971; Holčík 1977; Nagięć 1977; Popova and Sytina 1977).

Food consumption depends on temperature and food supply (Swenson 1977). The daily ration of predatory percids during the growing season under optimal feeding conditions amounts to about 3–7% of the body weight (Popova and Sytina 1977; Thorpe 1977a; Swenson 1977). Excess feeding at optimum temperatures results in daily rations of 11% (Willemsen 1977), whereas the daily ration for plankton-feeding perch fingerlings reaches a level of 28% (Spanovskaya and Grygorash 1977). Under good feeding conditions, pikeperch and perch consume annually at least 220% of their body weight (Popova and Sytina 1977). Evacuation rate depends strongly upon temperature, prey size, and species (Popova and Sytina 1977; Molnar et al. 1967; Schneider 1973; Swenson and Smith 1973; Thorpe 1977c).

Food conversion is temperature independent at temperatures well within the "normal" range. Rates under optimum feeding conditions vary little between species: 4–5 for pikeperch, 4–5.5 for perch (Popova and Sytina 1977; Willemsen 1977), and 4.5–6 for walleye (Swenson 1977).

Feeding activity of percids is connected with adaptation to low light intensities, often leading to two main feeding periods: early morning and evening. Pikeperch usually are inactive during daytime (Popova and Sytina 1977; Rundberg 1977). Walleye are limited in their activities by intensive light and are primarily nocturnal feeders upon pelagic prey, though they may feed at midday on demersal prey at low food densities (Swenson 1977). Sauger are still more adapted to darkness and feed in deeper water; in shallow water their activity increases with wind (Swenson 1977). Fingerlings of Eurasian perch during the plankton-feeding stage show two peaks in activity (early in the morning and in the evening) but during the benthos-feeding stage feed only in the morning (Spanovskaya and Grygorash 1977). In adult perch a frequent pattern of midmorning and evening peaks of feeding activity may sometimes be masked, especially among piscivorous individuals, by the irregularity of prey availability (Thorpe 1977a).

Migration — Percids generally do not move long distances. The main pattern is migration during the period before spawning towards the spawning grounds, and after spawning, a gradual dispersion over the feeding area. Onshore spawning migrations in the spring may be guided by temperature gradients in the direction of optimal temperatures for gamete viability and embryo survival (Rawson 1957; Belyy 1963; Forney 1967; Priegel 1970). The Etheostomatini generally move upstream (or into shallower waters in lakes) for spawning and then move back downstream or into deeper waters (Winn 1958a).

Fish tagged in the spawning area are frequently recovered from the same area during a following spawning season, thus strongly suggesting the existence of distinct spawning populations in walleye (Spangler et al. 1977) and pikeperch (Nagięć 1977). Walleye seem in many waters to be less migratory: Most tagged fish were recovered not farther away from the tagging site than 8 km (Atton and Kallemeyn unpublished data; Schupp and Macins 1977; Spangler et al. 1977), but migrations over some hundreds of kilometres are mentioned by Ferguson and Derksen (1971) and Schneider and Leach (1977) in the Great Lakes.

Migrations of yellow and Eurasian perches are also restricted (Bagenal 1977; Henking 1923; Mraz 1952; Kozikowska 1966). Although distances of 70 km can be covered, perch maintain a preference for their "own" area of the lake: Even when transported over distances of about 30 km, they showed, like pikeperch, a distinct tendency for homing (Willemsen 1977). This limited migratory behavior may even lead to different morphological groups within a lake (Chikhova 1973). Pikeperch are more migratory than perch, but despite some exceptionally long migrations of up to 82 km (Lind 1977) and 120 km (Svärdson and Molin 1973) the average migration distance does not exceed 10–20 km (Lind 1977; Rundberg 1977; Willemsen 1977).

Sauger are the most migratory of this group: Recoveries from tagged fish showed that distances up to about 380 km were covered at minimal mean swimming speeds of 19.7 km/day upstream and 21.1 km/day downstream (Fitz and Holbrook unpublished data). Vertical migration is the result of avoidance of high light intensities and low temperatures, and the presence of food and sufficient oxygen. Especially in clear water, walleye and sauger tend to stay in deeper layers at midday, but still above the thermocline (Fitz and Holbrook unpublished data; Swenson 1977; Hokanson 1977; Rundberg 1977).

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Factors Influencing Year-Class Strength of Percids: A Summary and a Model of Temperature Effects[1]

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Factors regulating year-class strength in the percid genera *Stizostedion* and *Perca* are summarized. Some index of water temperature regime correlates significantly with year-class strength of percids in many water bodies. Moderate synchrony of year-class strength is noted for walleye (*Stizostedion vitreum vitreum*) in several lakes in North America. A probablistic model is proposed to explain the basis of temperature dependence of year-class strength in percids, but tests of the model using Lake Erie data indicated that observed correlations between temperature and year-class strength of yellow perch (*Perca flavescens*) and walleye may not be the result of direct effects of the temperature regime on survivorship of early life-history phases.

Key words: Percidae, year-class strength, temperature, probalistic model, early life history

KOONCE, J. F., T. B. BAGENAL, R. F. CARLINE, K. E. F. HOKANSON, AND M. NAGIĘĆ. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. J. Fish. Res. Board Can. 34: 1900–1909.

Nous résumons les facteurs contrôlant l'abondance des classes d'âge des genres de percidés *Stizostedion* et *Perca*. Dans plusieurs plans d'eau, il y a corrélation significative entre un indice du régime des températures de l'eau et l'abondance des classes d'âge de percidés. On note une synthconie modérée dans l'abondance des classes d'âge du doré jaune (*Stizostedion vitreum vitreum*) dans plusieurs lacs nords-américains. Nous proposons un modèle probabiliste pour expliquer comment l'abondance des classes d'âge des percidés dépend de la température. Mais des essais du modèle avec des données du lac Erié indiquent que les corrélations observées entre la température et l'abondance des classes d'âge tant de perchaudes (*Perca flavescens*) que de dorés jaunes peuvent ne pas être le résultat d'effets directs du régime de températures sur la survie au début du cycle biologique.

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IN this paper we summarize the major factors thought to regulate year-class strength in the genera *Stizostedion* and *Perca*. We also report a tentative pattern of year-class synchrony in North America and advance a model based on the temperature dependence of mortality in early life history to explain variation in the year-class strength of species in these two genera.

Contributions to the PERCIS Symposium revealed the universality of fluctuations in year-class strength in populations of species in the two

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genera. The phenomenon was mentioned in at least 23 of the papers presented, which represented water bodies varying in area, depth, flushing rate, intensity of exploitation, and the species composition of associated fishes. For the Eurasian species, the range of the fluctuation was greater for Eurasian perch (*Perca fluviatilis*) than for pikeperch (*Stizostedion lucioperca*). In Lake IJssel, for example, Willemsen (1977) reported that the ratio of the strongest to weakest year-class was 100 for perch and 20 for pikeperch. Kipling (1976) reported a large (400-fold) variation in perch year-class strength in Lake Windermere and year-class strength fluctuations of pikeperch have been observed to range from 10-fold to 55-fold in other European water bodies (Boiko 1964; Lind 1977; and Rundberg 1977). In North America, yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) have similar patterns of fluctuation of year-class strength. Yellow perch year-class strength has been reported to vary from 8-fold to 40-fold (Forney 1976; Smith 1977; Eshenroder 1977; Nelson and Walburg 1977). Walleye, in comparison, is reported to have year-class strength fluctuations of 12-fold–74-fold (Spangler et al. 1977; Smith 1977; Forney 1976; Carlander 1977; Kempinger and Carline 1977; Nelson and Walburg 1977; Busch et al. 1975). In some lakes yellow perch seem to have a greater variation in year-class strength than walleye (Forney 1976; Smith 1977), but the pattern is reversed elsewhere (Leach and Nepszy 1976).

Attempts to analyze the patterns of fluctuation ultimately are limited by the variation in methods of estimating year-class strength. Methods used include year-class contribution to a fishery, catch per unit effort for reference gears, mark-and-recapture technique, and trawl catches of year 0 juveniles. Not all of these methods yield the same estimates of year-class strength (e.g. Forney 1976). Thus, the comparison between water bodies of the amplitude of fluctuation in year-class strength of any species is limited. Nevertheless, the year-class strength of these fishes appears to be fixed either by the year 0 juvenile stage (Busch et al. 1975; Willemsen 1977) or by midsummer of the 2nd yr, year 1 juveniles (Forney 1976).

Factors Associated with Year-Class Strength

Various factors have been associated with the determination of year-class strength in percids. The most important physical factors appear to be water temperature, wind, and water level of lakes or flow rate of rivers. Less often, reports mention water transparency, oxygen concentration, and siltation of spawning grounds. Biotic factors include predation, cannibalism, prey availability, and size of spawning stock or stocking intensity. Although all of these factors may be interrelated, the water temperature regime may affect mortality rates directly or indirectly through any of the other factors and may thus be an ultimate cause of variation in year-class strength for many water bodies.

Most studies we reviewed implicated water temperature as a dominant factor regulating year-class strength. Using a variety of measures of the temperature regime, many authors found a positive correlation between water temperatures and survivorship of one or more development phases. Busch et al. (1975) found strong correlations between rates of spring warming and both total egg production and fry densities for a 10-yr period in Lake Erie. Eshenroder (1977) reported a similar relationship for yellow perch in Saginaw Bay for a 24-yr period. Nagięć (1977) reported the highest correlation between mean monthly temperature during spawning and incubation and the abundance of pikeperch year-classes. Positive correlations between air temperature and year-class strength were also reported (Svardson and Molin 1973), but other attempts to find correlations with air temperature have not produced significant relationships (Doan 1942; Jobes 1952; El-Zarka 1959; Heyerdahl and Smith 1971).

Apart from these attempts to find correlations, some studies showed the climatic regime to act on year-class strength in a discontinuous manner. Periods of cold weather, for example, seem to be associated with weak year-classes (Derback 1947; Smith and Krefting 1953; Walburg 1972). Bagenal (1977) and Kipling (1976) showed that weak year-classes of perch in Lake Windermere are always associated with cold summers (<150 degree-days above 14°C). Other authors noted that warm summers seem to produce strong year-classes (Payne 1964; Kuznetsov 1970). Only three studies in the PERCIS Symposium indicated lack of any relationship with water temperature (Carlander and Payne 1977; Kempinger and Carline 1977; Willemsen 1977).

The importance of the other physical factors (wind, water level, and flow rate) appeared to be less general. Mean daily wind velocity accounts for much of the variation in survival of early stages of yellow perch in Oneida Lake (Clady 1976), but in other studies wind does not correlate significantly with strength of year-class (Busch et al. 1975). For river spawning populations of walleye, Spangler et al. (1977) reported a positive relationship between flow rate and strength of year-class. A positive association between water level and year-class strength in walleye and pikeperch has also been reported for several water bodies: reservoirs on the Missouri River (Nelson and Walburg 1977); reservoir of Kaunas, Lithuania (Virbickas et al. 1974); Rainy Lake, Ontario, which has water level regulated by a dam (Chevalier 1977); the delta of the Neman River in Lithuania (Virbickas et al. 1974); lakes with substantial marshes (Clear Lake, Iowa, Carlander and Payne 1977; Lake Winnebago, Wisconsin, Priegel 1970); and some Swedish lakes (Svardson and Molin 1973).

Analysis of biotic factors regulating year-class strength is complicated by the predator–prey relationships for *Stizostedion* and *Perca* species. All species of these two genera are both potential predators as well as potential prey. As adults, they prey on several fish species, if available, and they shift readily to cannibalism. They are especially vulnerable to predation in the 1st yr of life. Forney (1977) concluded that prey availability regulates both growth of adult walleye and walleye year-class strength in Oneida Lake. Willemsen (1977) observed an analogous relationship between smelt and pikeperch in Lake IJssel. These studies imply a possible self-regulation mechanism for percid populations. In some unexploited populations of salmonids, large standing stocks of adults suppress recruitment (Johnson 1976). A similar regulation method has been observed in ponds in which perch is the only fish species (Alm 1951; Menshutkin and Zhakov 1964; Sumari 1971). In these cases, a single year-class predominates and other strong year-classes only occur when the density of the dominant year-class drops to some low level.

Prey availability may also influence year-class strength. The most critical aspect of food availability seems to be the timing of specific preferred food (Menshutkin et al. 1968; Momot et al. 1977; Nagięć 1977; Willemsen 1977). Hokanson (1977) showed food density to be important to initiation of feeding and survival of pelagic larvae of yellow perch. In studies of competitive interaction, Johnson and Hale (1977) reported a 15-fold increase in yearling yellow perch and walleye following white sucker (*Catostomus commersoni*) removal from Wilson Lake, Minnesota. Johnson (1977) observed a decrease in walleye density with increasing density of smallmouth bass (*Micropterus dolomieui*).

Stock–recruitment relationship are not obvious for these percids. Some observations indicated a positive relationship between brood-stock density and year-class strength (Chevalier 1977; Busch et al. 1975; Shuter and Koonce 1977). But others found either no relationship or a negative one (Willemsen 1977; Smith 1977; Schneider and Leach 1977; Eshenroder 1977; Bagenal 1977).

Generality of Year-Class Strengths

From the assembled expertise at the PERCIS Symposium we attempted to find a pattern of year-class strengths common to various lakes. Because of the major importance of water temperature, we reasoned that climatic effects might show some consistency within certain geographical areas. We polled individuals to determine the years in which strong year-classes of any percid species were observed in the water bodies for which they had data. We obtained these estimates (Table 1) for 10 European lakes and 18 lakes and bays of large lakes in North America. Among the North American lakes, we observed a moderate synchrony. At least 20% of the lakes represented had strong year-classes of walleye in 1954, 1959, 1962, 1965, and 1972. The appearance of this synchrony is noteworthy, but the kind of information we acquired needs more careful review. In retrospect, we should have also surveyed weak year-class timing. Nevertheless, the data we have suggest some underlying trends, which were also noted by Eshenroder (1977), and should be developed more rigorously in future work.

Probabilistic Model of Year-Class Strength in Percids

Factors associated with year-class strength may be applied in a probabilistic manner to a sequence of development phases (Fig. 1). To use this conceptual model, we evaluated the direct effects of water temperature on survivorship of early life-history stages of yellow perch. Other factors such as food availability, predation, and cannibalism, which are also temperature dependent, may modify these survival probabilities, but insufficient data exist to evaluate their regulatory role with this model. The following discussion presents the assumptions and data used to construct a model from the concepts in Fig. 1.

Spawning and maturation — Hokanson (1977) summarized information available on the role of temperature in the production of viable eggs. Spawning temperature is a complicated function of an organism's temperature history. To initiate the model, therefore, we assumed a stock-specific optimum spawning temperature of 5°C. Time of spawning is estimated from a temperature record for a specific lake, and viability is assumed to be 60%.

Probability of surviving cleavage-egg phase — The time required to complete this phase is a function of incubation temperature (Hokanson 1977). However, temperature of incubation also

TABLE 1. Years during 1940–76 in which strong year-classes of percids[a] were reported in the PERCIS Symposium for various European and North American Lakes. Within each group, lakes are listed in order of increasing latitude.

Lake	Year																																				
	1940	1	2	3	4	5	6	7	8	9	1950	1	2	3	4	5	6	7	8	9	1960	1	2	3	4	5	6	7	8	9	1970	1	2	3	4	5	6
European lakes																																					
Baalton													0								0				0				0								
Constance																												X				X		X			
Klivaca																				X	X						X										
IJssel		0				0		0	0		0																			0,X	X	X		0,X	X	0,X	0,X
Jesiorak														0														0		0			0				
Windermere		X			X					X						X				X																	
Loch Leven																									X				X			X					
Hjälmaren														0						0							0			0						0	
Mälaren														0		0				0							0	0		0							
Kolliolamni																												X									
North American lakes																																					
Norris Res.																															W						
Erie															W		W			W			W			W					W		W		W		
St. Clair															W		W			W			W			W					W		W		W		
Clear Lake									W	W	W	W															W			W			W				
Bay of Quinte														W				W		W																	
Oneida														W				W		W	W		W		W			W	W			W					
Huron																				W			W			W				W						W	
Georgian Bay																W				W	W					W											
Winnebago																				W																	
Pike Lake																				W																	
Green Bay					W					W	W	W																									
Oahe																														W			W	W			
Escanaba																				W			W			W											
Mille Lacs															W					W																	
Leech																								W			W										
Red Lakes						W	W						W		W																						
Lake of the Woods																								W			W										

[a] X, *Perca fluviatilis*; 0, *Stizostedion leucioperca*; W, *Stizostedion vitreum vitreum*.

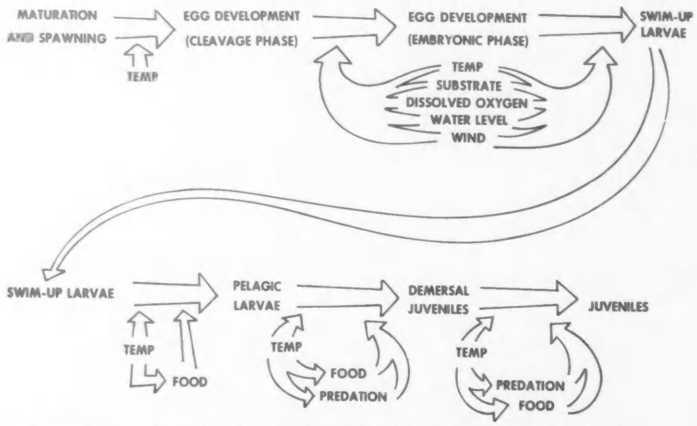
MATURATION
AND SPAWNING
TEMP
EGG DEVELOPMENT
(CLEAVAGE PHASE)
EGG DEVELOPMENT
(EMBRYONIC PHASE)
SWIM-UP
LARVAE
TEMP
SUBSTRATE
DISSOLVED OXYGEN
WATER LEVEL
WIND
SWIM-UP LARVAE
TEMP
FOOD
PELAGIC
LARVAE
TEMP
FOOD
PREDATION
DEMERSAL
JUVENILES
TEMP
PREDATION
FOOD
JUVENILES

FIG. 1. Interactions of factors that determine year-class strength of *Perca* and *Stizostedion* species.

affects survival (Hokanson and Kleiner 1974). Using these two relationships, we relate the probability of survival through this stage by

$$(1)\quad P_1 = 1 - \sum_{i=1}^{n} {}^1D_i$$

where n is the number of days required to complete the phase and ${}^1D_i$ is the temperature-dependent death rate calculated from Hokanson (1977). Because the time required to complete the phase is temperature dependent, we had to assume a daily rate of development, which is also temperature dependent. On a rising temperature regime, we considered the phase completed when the cumulative development equals or exceeds a value of 1.0. Temperature dependence of mortality rate is given in Table 2, and development rates at various temperatures are

Temp (°C)	Development rate (day^{-1})	
	Cleavage egg	Embryo
3	0.071	0.028
6	0.154	0.028
9	0.283	0.043
12	0.444	0.075
15	0.611	0.125
18	1	0.154
21	1	0.2
24	1	0.2
27	1	0.2
30	1	0.2

Probability of surviving the embryonic phase — We calculated survival of this phase in a manner similar to that for the cleavage-egg phase. Again using the data of Hokanson and Kleiner (1974) we implement the following function:

$$(2)\quad P_2 = 1 - \sum_{i=1}^{n} {}^2D_i$$

where n is the number of days required to complete the phase and ${}^2D_i$ is the temperature-dependent death rate. Development rates and death rates were computed from Hokanson (1977) as described above. Values for development rates are summarized above and mortality rates are given in Table 2.

TABLE 2. Daily mortality rates for phases of yellow perch from cleavage egg to swim-up larvae

Temp (°C)	Cleavage egg	Embryo	Swim-up larvae
3	0.050	0.027	1.0
6	0.005	0.018	0.85
9	0.003	0.018	0.42
12	0.000	0.015	0.12
15	0.050	0.019	0.02
18	0.160	0.008	0.0
21	0.70	0.020	0.08
24	1.0	0.150	0.20
27	1.0	0.2	0.45
30	1.0	0.2	1.0

Probability of surviving swim-up phase — The swim-up phase corresponds to the eleutheroembryonic phase described by Balon (1975). We treated the temperature dependence of survival in the same way as for egg development. Hokanson (1977) reported that development times for this phase were approximately 1 day and that survival was temperature dependent. We thus defined survival probability for this phase as

$$(3)\quad P_3 = 1 - {}^3D_i$$

where ${}^3D_i$ is the daily death rate (Table 2).

Probability of surviving pelagic larvae phase — We assumed that an individual larva starts this phase at some weight and continues in the pelagic phase until a minimum weight is achieved. The growth relationship is

$$(4)\quad B_t = B_0 e^{kg_m t}$$

where B_t is the weight per individual at time t, B_0 is the starting weight, k is the temperature-dependent fraction of maximum growth rate, and g_m is the maximum growth rate. The value of k depends on consumption and temperature in a manner similar to that developed by Kitchell et al. (1974, 1977):

$$(5)\quad k = pr_c - r_R$$

where p is a coefficient related to the availability of prey, and r_c and r_R are functions of temperature described by Kitchell et al. (1977). Parameter values are given in Table 3. We then estimate survival of the phase by

$$(6)\quad P_4 = e^{-\sum_{i=1}^{t_m} {}^4D_i}$$

where ${}^4D_i$ is the temperature-dependent death rate and t_m is the time required to complete the phase. The instantaneous daily mortality coefficients for various temperatures were calculated from McCormick (1976):

Temp (°C)	Instantaneous mortality (day^{-1})
3	0.0002
6	0.0002
9	0.0010
12	0.0058
15	0.0050
18	0.0030
21	0.0030
24	0.0040
27	0.0004
30	0.0002

Unfortunately, these mortality coefficients were obtained for juvenile yellow perch. We suspect the pelagic larvae to be more stenothermic, but no data are available to obtain more suitable parameters for the model.

TABLE 3. Parameter values for larval growth in equations 4 and 5. Both r_c and r_R are temperature dependent functions described by Kitchell *et al.* (1977).

Parameter	Value
g_m	0.052·day^{-1}
B_0	1.0 mg/ind
B_m	150.0 mg/ind
p	1.0[a]
	r_c constants
T_m	32.0°C
T_0	23.0°C
Q_{10}	2.3[a]
	r_R constants
R_m	0.14[a]
T_m	35.0°C
T_0	28.0°C
Q_{10}	2.1[a]

[a] Dimensionless constant.

Probability of surviving demersal juvenile phase — Fish in this phase have completed larval development and move from a pelagic to a demersal habitat. In our simulations we assumed that fish remain in this phase for the rest of the year to day 360. We also assumed that mortality during this phase depended on temperature, and the probability of survival was determined by

$$(7)\quad P_5 = e^{-(\alpha t_m + \sum_{i=1}^{t_m} {}^5D_i)}$$

where ${}^5D_i$ is the same temperature-dependent death rate used for the pelagic larvae and α is the base natural mortality, which we assumed to be 0.017·day^{-1}.

The relative year-class strength, or joint-survival probability, was calculated

$$(8)\quad P = P_1 \cdot P_2 \cdot P_3 \cdot P_4 \cdot P_5 \cdot 0.6$$

Actual year-class strength could be calculated from estimates of the density and fecundity of the brood stock. As a test of the model calibration, we compared (Fig. 2) the survival probabilities of the three early development phases of yellow perch with the experimental data of Hokanson and Kleiner (1974). The good agreement then allowed us to test the model on a variable temperature case.

Application of Model to Perch and Walleye in Lake Erie

We chose to test the model by comparing observed and predicted year-class strengths of perch and walleye in Lake Erie. Three factors

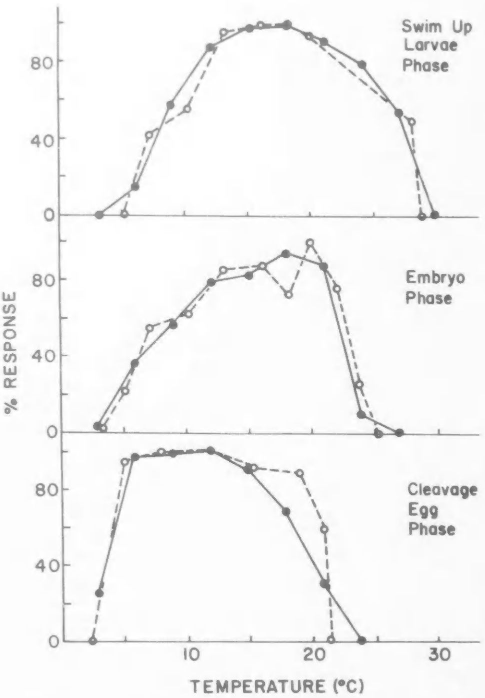

FIG. 2. Comparison of survival probabilities of early development phases of yellow perch predicted by model (●) and observed by Hokanson and Kleiner (1974) (○).

motivated this choice. First, year-class strength of walleye in the western basin of Lake Erie over the period of 1959–70 had a significant correlation to the temperature regime in the spring (Busch et al. 1975), and a similar relationship seemed to hold for perch (Hartman 1972). Second, daily temperatures of surface waters at South Bass Island were available for the period 1918–76 from the Ohio Department of Natural Resources (1961; and unpublished data). Third, the walleye and yellow perch populations in Lake Erie were highly exploited during this period. Under this condition we would expect recruitment to be most sensitive to climatic fluctuations. The application of this model for yellow perch and walleye assumed that the two species have the same physiological dependence on temperature. Although Hokanson (1977) suggested that walleye may be a few degrees less tolerant than yellow perch, Kitchell et al. (1977) were successful in describing temperature dependence of walleye growth using parameters derived for perch. Thus, given the similarity in their ranges and life history we considered that this assumption was not unreasonable.

Predicted survival of the early life-history stages of both yellow perch and walleye did not agree with the observed patterns of year-class strength in the western basin of Lake Erie. The joint-survival probability for 1959–70 had a relatively narrow range, 0.087 in 1967 to 0.132 in 1960 (Table 4), which contrasts with the 74-fold range for walleye and 18-fold range for yellow perch (Table 5). Using a nonparametric measure of rank correlation (Spearman r_s, Conover 1971), no significant correlation could be detected between predicted survival and observed year-class strength of either yellow perch or walleye, but

TABLE 4. Predicted survival probabilities of various life-history stages of yellow perch and the joint-survival probability (P) of the early life history from egg fertilization through age 0 juveniles, 1960–70. Life-history intervals reported are cleavage egg (P_1), embryo (P_2), swim-up larvae (P_3), pelagic larvae (P_4), and age-0 juvenile (P_5).

Year	P_1	P_2	P_3	P_4	P_5	P
1960	0.971	0.695	0.895	0.997	0.366	0.132
1961	0.979	0.654	0.922	0.997	0.370	0.131
1962	0.972	0.640	0.911	0.996	0.347	0.118
1963	0.963	0.619	0.847	0.996	0.335	0.101
1964	0.954	0.639	0.924	0.996	0.334	0.112
1965	0.953	0.692	0.917	0.996	0.343	0.124
1966	0.903	0.614	0.815	0.999	0.350	0.095
1967	0.971	0.572	0.736	0.997	0.354	0.087
1968	0.974	0.715	0.906	0.997	0.341	0.129
1969	0.970	0.601	0.870	0.997	0.376	0.114
1970	0.972	0.660	0.901	0.997	0.331	0.114

TABLE 5. Rates of spring warming and indices of year-class strength in walleye and yellow perch of western Lake Erie, 1960–70.

Year	Rate of warming (°C/day)[a]	Walleye[b]	Perch[c]
1960	0.18	0.4	420
1961	0.24	7.8	1300
1962	0.29	29.6	2800
1963	0.20	1.5	210
1964	0.32	11.0	330
1965	0.36	11.1	2300
1966	0.10	0.6	160
1967	0.13	3.4	340
1968	0.12	1.7	160
1969	0.24	5.2	180
1970	0.31	28.2	640

[a] Mean daily rate of temperature increase from April to mid-May (Busch et al. 1975).

[b] Number of young-of-the-year walleye caught per hour of trawling (from Busch et al. 1975).

[c] Number of young-of-the-year perch caught per hour of trawling (from Leach and Nepszy 1976).

significant correlations are found for rate of spring warming and both walleye and yellow perch year-class strength and for walleye year-class strength and yellow perch year-class strength:

	Correlation coefficient	
Comparison	r_s	P
Predicted survival vs. walleye YCS	0.091	>0.1
Predicted survival vs. yellow perch YCS	0.382	>0.1
Walleye YCS vs. yellow perch YCS	0.664	<0.025
Rate of warming vs. walleye YCS	0.841	<0.001
Rate of warming vs. yellow perch YCS	0.682	<0.025

The correlation between rate of spring warming and walleye year-class strength is consistent with the observations by Busch et al. (1975).

Although the predicted survival probabilities did not correlate significantly with observed walleye year-class strength, predictions of the timing of the hatch were much better. Predicted hatching of walleye (swim-up phase) occurred over a range of April 27–May 15, and the observed range of midhatching for the same period was May 1–12 (Busch et al. 1975):

Year	Observed date of midhatching	Predicted date of hatching
1960	May 10	May 8
1961	May 12	May 15
1962	May 4	May 4
1963	May 3	May 1
1964	May 7	May 9
1965	May 11	May 11
1966	May 8	May 4
1967	May 8	May 1
1968	May 1	April 27
1969	May 6	May 5
1970	May 11	May 5

Thus, the temperature dependence of development seemed to be more accurately described than survivorship.

Discussion

Our simulation results indicate that direct temperature effects on mortality of various early life-history phases of perch and walleye may not determine the year-class strength in western Lake Erie. Although the model accounts for about 90% of the mortality as due to temperature dependence of mortality, the narrow range of the joint-survival probability and the absence of any significant correlation of joint-survival probability to observed year-class strength argue against a regulatory role for the temperature regime. In fact, the relatively high survival probabilities through the pelagic larvae phase may indicate that the temperature regime in western Lake Erie is nearly optimal for normal development of perch and walleye.

A significant correlation between year-class strength of these fishes and temperature regime could result from climatic influences on other aspects of population regulation. Spawning behavior, for example, may be affected by the weather conditions during a 2-wk period in the spring. Busch et al. (1975) reported significant correlations between rate of warming and both egg deposition and year 0 juvenile density, which is a good predictor of year-class strength. Rank correlation of year-class strengths indicated by egg deposition and year 0 juvenile density is significant ($r_s = 0.64$, $P < 0.025$). Thus the relative year-class strength in Lake Erie appears to be fixed before our simulations started.

Our results, therefore, suggest that temperature may limit year-class strength directly only under severe climatic regimes. These regimes occur with greatest frequency at the northern and southern boundaries of the ranges of these percid species, but may also occur periodically elsewhere (cf. Kipling 1976). The model might be used to explore range limitation or to determine possible effects of thermal stress. The occurrence of significant correlations between year-class strength and temperature in the middles of the ranges of these species, however, cannot be explained by the model we formulated. Spawning behavior, availability of specific types of food at various critical phases of development, predation and cannibalism rates, mortality of adults, and various abiotic factors may also have some correlation with temperature or act synergically with the physiological effects of temperature. Temperature effects on growth rate (e.g. Kitchell et al. 1977), for example, may prolong exposure to some other mortality factor.

Many of these interactions might be evaluated with the type of model developed here. For instance, joint effects of temperature and food density on growth and survival probabilities of larval percids could be incorporated by using some bio-energetic model (e.g. Brett et al. 1969; Kitchell et al. 1974; Kitchell et al. 1977). Inclusion of predation models that relate survival probabilities to development phase, temperature, alternative prey densities, and predator density (e.g. Menshutkin et al. 1968) might expand the use of this model to examine the role of predation and cannibalism in regulating year-class strength. Unfortunately, sufficient data to support these model extensions is rarely available for any single percid population. Data requirements include stock size, age distribution, recruitment, seasonal temperature regime at location of fish stock, spawning time and temperature, periods of occurrence of various development phases, specific food biomass, and predator density. While it might be said that the existence of such data sets would obviate the need for a model, this approach or a similar one proposed by Kipling (1976) may nevertheless aid future experimental design in sorting out causal relationships.

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Reproductive Guilds of Percids: Results of the Paleogeographical History and Ecological Succession[1]

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A holistic picture of the Percidae is attempted, exploring the theory of reproductive guilds. Seven guilds encompass all 163 species; forms related closely in terms of Linnean taxonomy may belong to very different guilds. Adaptations in spawning ground selection, other reproductive behavior and morpho-physiological features of early ontogeny all center on respiration and protection against predators. The adaptation of guarding enables survival in low densities as well as in an environment with decreasing oxygen content, or enables invasion of such an environment. The paleogeographical origin and distribution of percid fishes are reconstructed along these lines. Over the short term, guild succession is enhanced by changes in fluvial gradient and lake metabolism.

Key words: Percidae, succession, reproductive guilds

BALON, E. K., W. T. MOMOT, AND H. A. REGIER. 1977. Reproductive guilds of percids: results of the paleogeographical history and ecological succession. J. Fish. Res. Board Can. 34: 1910–1921.

Nous essayons de présenter ici un tableau holismique des Percidae, en explorant la théorie des confréries reproductrices. Sept confréries englobent toutes les 163 espèces; des formes qui, en termes de classification linnéenne, sont étroitement apparentées peuvent appartenir à des confréries très différentes. Les adaptations dans le choix des frayères, dans le reste du comportement reproducteur et dans les caractères morphophysiologiques du début de l'ontogénie sont tous axées sur la respiration et la protection contre les prédateurs. Monter la garde est une adaptation qui permet la survie à de faibles densité de population, tout comme dans un environnement à teneur en oxygène décroissante, ou permet l'invasion d'un tel environnement. Nous reconstituons l'origine paléogéographique et la répartition des percidés suivant ces lignes. Des changements dans le gradient fluvial et le métabolisme des lacs favorisent, à court terme, la succession de confréries.

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IN this paper we attempt to provide an integrated holistic picture of the Percidae even though the necessary data on reproductive styles and early ontogeny are not available for many species. The reproductive guild approach, we believe, may be more meaningful than any other relatively simple approach in understanding reasons for success of various fish taxa in rivers and lakes within the "normal" spectrum of such habitats.

To understand the concept of the reproductive guilds of fishes, the initial proposal (Balon 1975a, b) may be consulted. Briefly, feeding styles of fishes have repeatedly been shown as not the only determinant of ultimate densities and structures of fish communities. Rather, some evidence points to reproduction and adaptations of early ontogeny as the main determinants. In effect, the phyletic order of guilds in each ethological section (Balon 1975a, Table 1), along with the r- and K-selection concept (MacArthur and Wilson 1967; Pianka 1970), spans the r–K

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

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continuum. For example, pelagophils are clearly r-selected and ostracofils K-selected, whereas nonguarders are on the r-selected side of the continuum in relation to the more K-selected character of guarders and bearers. Furthermore, "homing," expressed generally as a precise selection of spawning sites by adult fishes (Crossman 1977), can be and probably also is determined during early ontogeny.

As stated by Kryzhanovsky (1949), "adaptations of fishes for spawning and development reflect not only the essential ecological factors of the embryonic period, but also the essential factors of all the other intervals of life. These adaptations mark the biology of adults, and define the type of migrations, invasion abilities, and limits of distribution." In effect, we can concentrate on two factors only, predators and availability of oxygen, and consider the extraordinary variety of other natural factors to be associated with these two prime factors.

The walleye (*Stizostedion vitreum vitreum*) and the pikeperch (*S. lucioperca*) provide leading examples. The North American walleye is limited to well-oxygenated and turbulent spawning grounds where survival of sufficient numbers depends entirely on water conditions and concentration of spawners (Regier et al. 1969). A single pair probably can not reproduce successfully. The European pikeperch developed adaptations which enable it to become independent of the fluvial environment; nest building and guarding of the eggs enable it to expand the spawning grounds into less well oxygenated waters with silted or muddy bottoms. This protection against predators guarantees survival of sufficient numbers so that a single pair can ensure successful reproduction. Hence the walleye and pikeperch, although closely related in terms of Linnean taxonomy, belong to different guilds (and ultimately one is an r- and the other a K-selected species, although their adult sizes are equal).

Characteristics of Percid Guilds

The approximately 21,000 species of living fishes (Cohen 1970) can be placed in 32 ecoethological guilds (Table 1). The 163 species of Percidae (Collette and Bănărescu 1977) belong to seven of these guilds. As already stated, forms morphologically closely related often belong to quite different guilds. Assuming that the direction of evolution of reproductive styles followed the vertical arrangement of Table 1, it appears that in some instances reproductive adaptations first acted to separate taxa even before morphological separation took place (see, for example, the morpha or infraspecies or ecotype concepts in Berg 1948). Consequently this process is of great ecological significance. The European and yellow perch may form an exception to this rule. Despite a similar biology, including reproductive style (Thorpe 1977), morphological differences may justify taxonomic separation (Collette and Bănărescu 1977).

The first, most primitive (but see Balon 1975a, p. 860) section of nonguarders (A) includes all but two of the percid guilds. Among the nonguarders, four guilds are in the subsection of the most primitive open-substratum spawners (A.1) and one in the subsection of brood hiders (A.2).

The North American species *Stizostedion canadense* and *S. vitreum* belong to the simplest and most vulnerable guild of lithophils (A.1.3). They scatter eggs mainly on rock, rubble, or gravel bottoms, in turbulent areas of streams, rivers, or lakes (e.g. Fish 1932). Embryos hatch very early and require well-oxygenated water, as embryonic respiratory organs are only weakly developed. Both melanin and carotenoid pigments appear relatively late (Fig. 1). The eleutheroembryos (Balon 1975c) hide at the bottom for several days after hatching before schools are formed in shallow areas. Sauger embryos hatch earlier in spring and are at that time less developed and have more yolk than that of the walleye (Nelson 1968). This implies that the sauger is the more primitive of these two and the closer to ancestral pelagophils, whereas the walleye has come closer to the more advanced styles of percid reproduction. Instead of guarding, as in pikeperch, walleye, and sauger developed aggregations of spawners on spawning grounds to ensure spawning success. The sauger lags behind the walleye in this behavioral adaptation in that sauger spawning aggregations are apparently less well organized. The sauger spawns in smaller aggregations than walleye. On the other hand, the preserved sauger eleutheroembryo (Fig. 1b) looks more like the eleutheroembryo of the pikeperch (Fig. 1) but this proves to be not so when drawings from live specimens are compared (Fig. 2). In addition the eleutheroembryos swim up immediately after hatching. If true, this indicates an advanced trend compared with the walleye. For the time being, however, we shall assume the sauger to be more primitive in its overall reproductive style.

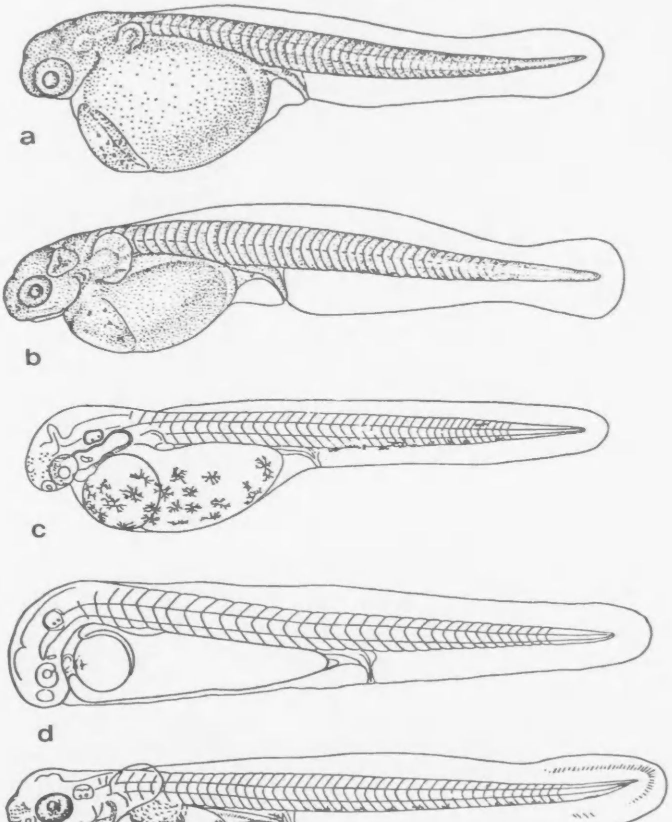
Gymnocephalus spp., *Percarina* spp., *Perca* spp., and, for example, *Etheostoma exile* are less specialized than the *Stizostedion* species discussed above. They are intermediate between the former and following guilds, they are a step further from their fluvial dependence and closer to more lentic

TABLE 1. Reproductive guilds of all living fishes with respective percid taxa (but only some examples of Etheostomatini) and areas of their distribution (E = Europe, NA = North America).

Section		
Subsection	Guild	Percid taxa
A. Nonguarders		
A.1 Open-substrate spawners	A.1.1 Pelagophils	
	A.1.2 Litho-pelagophils	
	A.1.3 Lithophils	*Stizostedion canadense* NA *Stizostedion vitreum* NA
	A.1.4 Phyto-lithophils	*Stizostedion marinum* E *Stizostedion volgense* E *Gymnocephalus* spp. E *Percarina* spp. E *Perca* spp. E+NA *Etheostoma exile* NA
	A.1.5 Phytophils	*Etheostoma microperca* NA
	A.1.6 Psammophils	*Ammocrypta* spp. NA *Percina caprodes* NA
A.2 Brood hiders	A.2.1 Lithophils	*Zingel* spp. E *Romanichthys* sp. E *Etheostoma caeruleum* NA *Percina copelandi* NA *Percina maculata* NA *Percina shumardi* NA
	A.2.2 Speleophils	
	A.2.3 Ostracophils	
	A.2.4 Aero-psammophils	
	A.2.5 Xerophils	
B. Guarders		
B.1 Substrate choosers	B.1.1 Lithophils	
	B.1.2 Phytophils	
	B.1.3 Aerophils	
	B.1.4 Pelagophils	
B.2. Nest spawners	B.2.1 Lithophils	
	B.2.2 Phytophils	*Stizostedion lucioperca* E *Etheostoma blennioides* NA
	B.2.3 Psammophils	
	B.2.4 Aphrophils	
	B.2.5 Speleophils	*Etheostoma* (*Catonotus*) NA *Etheostoma nigrum* NA *Etheostoma vitreum* NA
	B.2.6 Polyphils	
	B.2.7 Ariadnophils	
	B.2.8 Actinariophils	
C. Bearers		
C.1 External	C.1.1 Transfer brooders	
	C.1.2 Forehead brooders	
	C.1.3 Mouth brooders	
	C.1.4 Gill-chamber brooders	
	C.1.5 Skin brooders	
	C.1.6 Pouch brooders	
C.2 Internal	C.2.1 Ovi-ovoviviparous	
	C.2.2 Ovoviviparous	
	C.2.3 Viviparous	

habitats. Tentatively *Stizostedion marinum* and *S. volgense* can also be placed into this guild (Berg 1949) although additional (Heckel and Kner 1858; Antipa 1909; Berg 1949; Balon 1967a) evidence is needed to prove that they are really different from *S. lucioperca*. As phyto-lithophils (A.1.4), *S. marinum* and *S. volgense* still deposit eggs on available submerged plants in relatively clear water habitats, or on other submerged items such as logs, branches, gravel, or rocks. As a result they can utilize more area for spawning grounds and aggregate to a lesser degree than lithophils, most often only in polyandrous pursuits of a single female.

FIG. 1. Some percid eleutheroembryos at hatching: (a) *Stizostedion canadense*, 5.5 mm long; (b) *S. vitreum vitreum*, 6.8 mm (both from Nelson 1968); (c) *Gymnocephalus acerinum*, 4.3 mm; (d) *Percarina demidoffi*, 2.5 mm (from Kryzhanovsky et al. 1953); (e) *Perca fluviatilis*, 5.3 mm; (f) *Stizostedion lucioperca*, 4.6 mm (from Kryzhanovsky 1948); (g) *Etheostoma nigrum*, 5.0 mm (after Fish 1932 from Lippson and Moran 1974); (h) *Etheostoma vitreum*, 5.3 mm (after Kennedy 1965 from Lippson and Moran 1974). Members of four guilds are illustrated: a, b, the simplest lithophils (A.1.3); c, d, e, the phyto-lithophils (A.1.4); f, the guarding and nesting phytophil (B.2.2); and g, h, the guarding and nesting speleophils (B.2.5).


a
b
c
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h

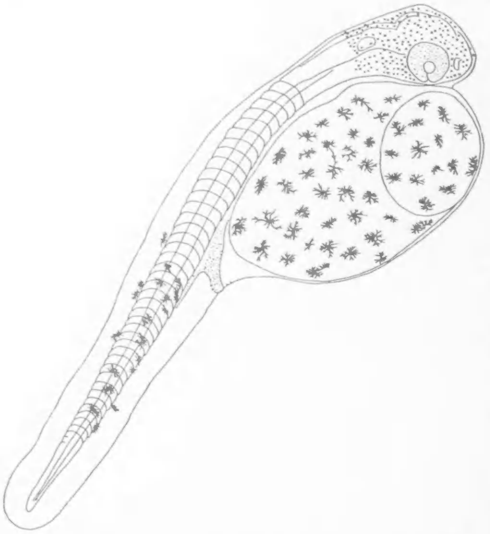

FIG. 2. However, a just-hatched eleutheroembryo of *Stizosterion vitreum vitreum* seen alive resembles *S. lucioperca* more than the drawings from preserved fish (Fig. 1b). Original drawing by James McElman.

Perch (at least *P. fluviatilis* and *P. flavescens*) may form a separate guild because of the special structure of the egg mass, the eggs not being deposited individually, but in long gelatinous ribbons with a system of interior passages and a special water-pumping arrangement enhanced by the vibratory consistency of the whole egg mass. Clearly, these gelatinous ribbons have a protective significance with a special solution to the oxygen supply. (Since they resemble gelatinous egg rafts or veils of some distantly related marine fishes (*Antennarius*, *Histrio*) we are tempted to see in this adaptation another proof of a close reproductive lineage between the ancestral serranid and perch.)

Phytophilous (A.1.5) percids are probably limited to some darters, for example, *Etheostoma blennioides* and *E. microperca*. Psammophilous forms (A.1.6) are *Ammocrypta* spp. and *Percina caprodes*. In both these guilds only North American percids are involved (Winn 1958a, b), contrary to the mixed North American and European character of phytolithophils (Table 1) and of the following guild.

The most diverse guild of percids are brood hiding lithophils (A.2.1). Details on early ontogeny and reproductive biology of most of these species are unknown and the placement into this guild was done rather on the basis of analogy and other evidence. Very little indeed is known about the Romanichthyini. This guild encompasses the three European species of *Zingel* and *Romanichthys valsanicola* as well as, for example, the North American species *Etheostoma caeruleum*, *Percina copelandi*, *P. maculata*, and *P. shumardi*. It represents the most common percid reproductive style. Interestingly, salmonids, which belong to the same guild also have this reproductive style. The evolutionary significance (late Pleistocene adaptation) of this analogy should not be overlooked (Balon 1968a). Eggs are hidden in natural or specially excavated places but they are usually not guarded except in some species which guard for a very short time after deposition. In most cases the eggs are buried in gravel. Eggs which are squirted into rock crevices or left to settle in cavities are in some species adhesive. In all cases, the hiding of eggs means that the eggs are placed in less favorable oxygen conditions and, therefore, require clean gravel or rocks in turbulent areas to ensure at least the minimum oxygen supply. Members of this guild as opposed to non-hiding percids are consequently limited in their choice of spawning places, but because their eggs are better protected (as in salmonids) the female is able to channel her reproductive energies into producing fewer but larger eggs with denser yolks than females in non-hiding percids. The surface of the yolk forms an expanded surface for a special respiratory network of vessels (Kryzhanovsky et al. 1953) supported in some cases by carotenoid pigments which help to release molecular oxygen when needed (Smirnov 1950, 1975; Soin 1956; Kostomarova 1962). In members of this guild the embryos hatch early but the eleutheroembryos are photophobic and disperse under the gravel to emerge only as large, fully formed and active alevins. This further decreases their mortality from predators.

Only a few percids evolved to the second section of guarders (B) and the even more advanced subsection of nest spawners (B.2). In all known cases the male percid is the nest building and guarding parent; hence, all are at the initial stage in the evolutionary progression of parental care (Barlow 1974). No known percids have progressed beyond guilds of this subsection.

The European species *Stizostedion lucioperca* may be placed in the guild of guarding and nest-spawning phytophils (B.2.2) (with certain reservations explained later). Circular nests are constructed on the bottom, amid algae and vascular plants whose roots are often exposed and used for attachment of adhesive eggs above the soft bottom. Unlike the more advanced members of this guild, e.g. some cichlids, pikeperch embryos do not have cement glands for attachment and swim up immediately after hatching (Kryzhanovsky et al. 1953). Their embryonic respiratory network of vessels on the yolk and finfold is not developed, and consequently the immediate upward swim to stay afloat is a prerequisite to avoid contact with the muddy bottom and to ensure a necessary amount of oxygen. The freshly hatched eleutheroembryos are too weak to gulp air through the membrane of the water surface. Therefore, air bubbles released by plants must be swallowed and have to enter the swimbladder before the connection between gut and bladder duct is lost (in a larva 7.5 mm long). Otherwise "the swimbladder remains empty because, for unknown reasons, its system of vessels cannot begin the gas secretion if the swimbladder is not filled beforehand with atmospheric gas via the mouth" (Kryzhanovsky et al. 1953, p. 51). To this guild belong some of the North American darters, for example, *Etheostoma blennioides*. Within this guild, the percids have little evolved beyond the most primitive features. Apparently pikeperch, within the area where it has lived the longest, i.e. the glacial refuges of the Danube (Kukuradze 1968) and the Volga Delta (Konstantinov 1957), constructs diligently guarded nests in shallow or freshly inundated areas. In some of the northernmost parts of its range nesting behavior of the pikeperch differs. The pikeperch often uses deep gravel or rocky bottoms for nest sites (Virbickas et al. 1974; Nagięć, personal communication), and in some instances no nest building or guarding occurs (Rundberg, personal communication). As discussed by Kryzhanovsky et al. (1953, p. 75), pikeperch developed nesting and guarding behavior, but its embryos and larvae are still similar to those of nonguarding and non-nesting percids (Fig. 1 and 2). Possibly here we touch on a general principle that the ethological part of the reproductive style evolves first, becoming fixed through selection before any related morphophysiological features.

Some North American darters (*E. flabellare*, *E. nigrum*, *E. vitreum*, and others) evolved the same (Page 1975) level of reproductive style as the pikeperch, utilizing natural cavities for nesting and guarding. However, these speleophils (B.2.5) advanced somewhat further in the sense that their ethological styles of nesting and guarding are accompanied by a better developed respiratory network on the yolk sac (Lippson and Moran 1974) and possibly by increased quantities of respiratory carotenoids; this is similar to other advanced guarders and nest spawners (Fig. 1).

Origin and Distribution of Percid Guilds

As far as we can generalize from existing evidence, percid fishes belong to only seven guilds within the first two sections of Table 1. Most are nonguarding, open-substratum spawners and brood hiders; only a few have evolved more advanced reproductive styles of guarders and nest spawners. There are no monophyletic guilds but some guilds are limited to North America or Eurasia.

The following general trend emerges. At first anadromous but later potamodromous primitive nonguarding open-substratum-spawning lithophils expanded to suitable spawning grounds with all the resultant adaptations of their embryos and larvae. Gradually phyto-lithophils, phytophils, and psammophils were formed. Only quite recently, parallel with the development of an extreme morphological specialization, further invasion of other spawning grounds has taken place along with better protection, and consequently a brood-hiding guild has developed in the North American Etheostomatini and European Romanichthyini. Guarding and nesting can be considered as a latest trend of percids to expand from their initial fluvial into an ever more lacustrine environment.

How does this apply through space and time? Collette et al. (1977) are obviously right in stating that there is very little fossil evidence that can be trusted, but whatever we believe about the validity of *Perca edlaueri* in the Paleodanube (Svetovidov and Dorofeyeva 1963) the fact remains that, except for the unique and specialized monophyletic Etheostomatini (forming the vast majority of species)[2], most taxa center on the Danube River area. *Perca*, for example, is represented here by the separate form *vulgaris*, and *Stizostedion* by three very different species, as are *Gymnocephalus* and *Zingel*. One exception is the unique genus *Romanichthys* (Fig. 3).

The basal percoid (serranid ?) from which, according to Collette and Banarescu (1977), the first paleopercid developed may have belonged to the most primitive guild of pelagophils (A.1.1.) and have inhabited the Tethys Sea in the Paleocene some 60 million years ago (formation of gelatinous egg rafts already by that time is possible). Consequently, as the dendritic Paratethys Sea lost more and more salinity, the first anadromous protopercid may have evolved there in the Eocene, some 50 million years ago. In the short, young rivers of this period a new guild may have evolved and so percid lithophils came into exis-

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[2] Possibly the North American Etheostomatini were given a chance to occupy a free benthic niche taken in Eurasia by Cobitidae. Explosive speciation is similar in darters and loaches within waters which formed glacial refugees. Darters and loaches are also similar in their body shapes and habitats.

TABLE 2. The evolution of percids in a geological time scale and in paleogeographic locations. (†means extinct.)

Environment	Migration	Percid	Guild	Area	Epoch	Million years B.P.
Marine	oceanodromous	serranid†	A.1.1	Tethys Sea	Paleocene	65
Marine and freshwater fluvial	anadromous	protopercid†	A.1.3	Paratethys	Eocene	58
Some marine, most freshw. fluvial	anadromous potamodromous	*Protoperca*† *Protostizostedion*†	A.1.3			
			→	across North Atlantic land route to NA		
		Perca†	A.1.3	Sarmat Sea to Ob Sea	Oligocene	36
Freshwater fluvial	potamodromous	*Stizostedion*†	A.1.3	Sarmat Sea & North America	Miocene	25
		Perca†	A.1.4	Paleodanube	Pliocene	13
		Perca		Danube Siberia	Pleistocene	1
			→	across Bering's land bridge to NA		
		Gymnocephalus	A.1.4	Danube	postglacial	0.012
		Percarina	A.1.4	Black & Azov S.		
		Etheostoma†	A.1.4	North America		
		Zingel	A.2.1	Danube		
		Romanichthys	A.2.1	Danube		
		Etheostoma	A.1.5	North America		
		Etheostoma	A.2.1	North America		
		Etheostoma	B.2.1	North America		
		Ammocrypta	A.1.6	North America		
		Percina	A.1.6	North America		
		Etheostoma	B.2.2 B.2.5	North America		
		Perca	A.1.4	Euroasia & NA		
		Stizostedion	A.1.3	North America		
		Stizostedion	A.1.4	Europe & Danube		
lacustrine		*Stizostedion*	B.2.2	Europe		

tence in a similar way as the later salmonids (Balon 1968a). Soon after, with the expanding river network across what is now Europe (Fink 1966; Balon 1967b, 1968b), the protopercid differentiated from its perchlike ancestor and formed an anadromous and potamodromous walleyelike fish. This fish was in turn able to invade North America via a land connection across the North Atlantic (Lindberg 1961). Let us date this tentatively in the upper Eocene and/or the lower Oligocene, some 40 to 30 million years ago. In the meantime, in the area of percid origin (Danube ?) the first, less specialized guild of phytolithophils (A.1.4) formed (Table 2). They were assisted in the Miocene by a further expansion of freshwater river networks within the branches, bays and coves of the Sarmat Sea and by the gradual formation of the Paleodanube River in the Pliocene, 25 to 10 million years ago. Thus the perch penetrated Siberia in the Oligocene and invaded North America via Pleistocene riverine connections at Beringia.

The other five, more advanced guilds of percid fishes apparently evolved independently on the two continents during the last interglacial or postglacial, as adaptations to more lentic environments which prevailed more and more with the aging of rivers and lakes. In other words, percids, along with other fishes, faced a need to adapt to less oxygen and to develop better protection against predation within more diverse fish communities (Fig. 4) or to give ground to more adaptable invaders. Along this evolutionary trend the more advanced guilds are clearly able to withstand more severe environmental sources of stress and are less vulnerable to the aging of their original fluvial environment than the guilds of nonguarders. The question to ask then is, given

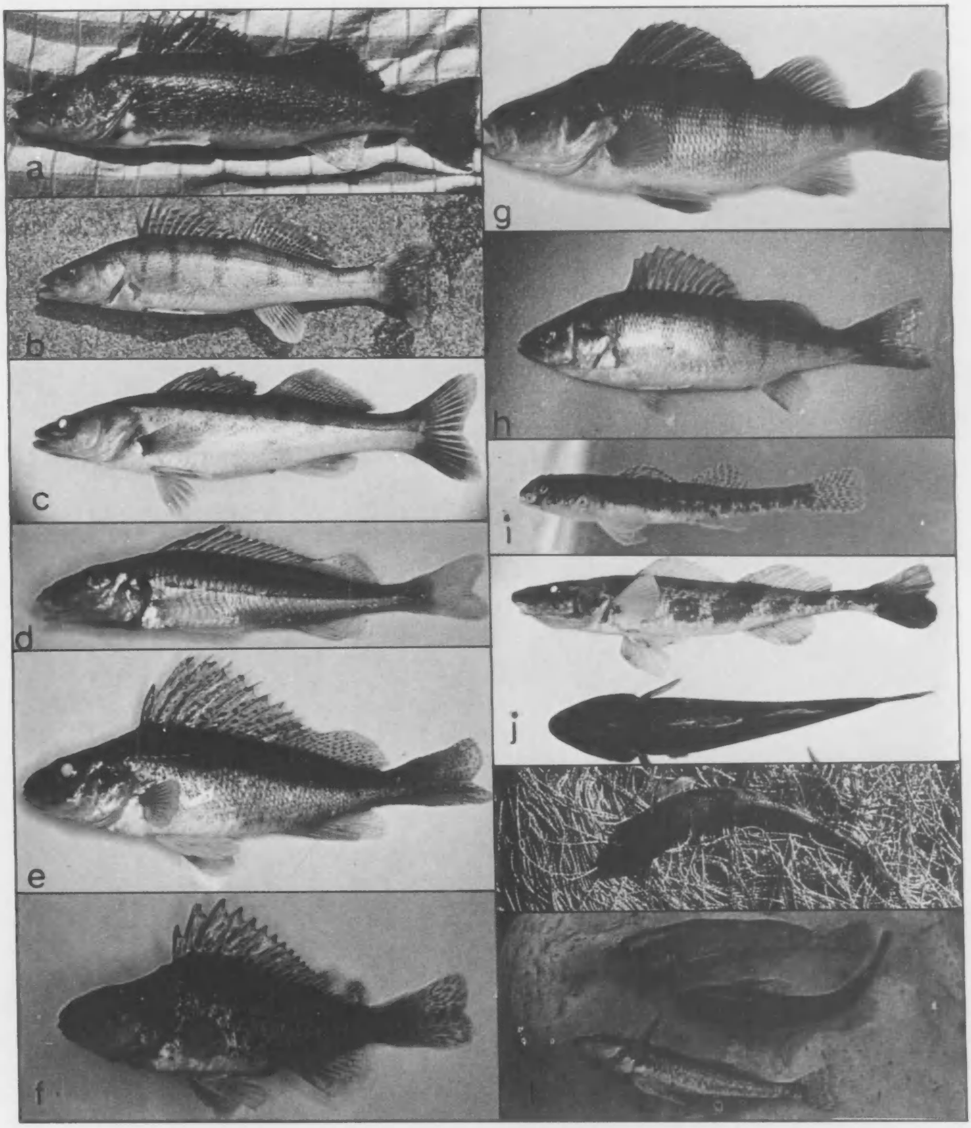

FIG. 3. Some percids in live colors: (a) *Stizostedion vitreum vitreum* from the Talbot River, Ontario, Canada; (b) *S. volgense*, (c) *S. lucioperca*, (d) *Gymnocephalus schraetser*, (e) *G. cernuum*, (f) *G. baloni*, and (g) *Perca fluviatilis vulgaris*, all from the middle Danube in Austria and Czechoslovakia; (h) *P. flavescens* and (i) *Etheostoma exile* from Lake Erie, Canada; (j) *Zingel zingel* and (k) *Z. streber* from the Danube River in Austria; and (1) *Romanichthys valsanicola* from the Argeş River in Roumania. All photographs by E. K. Balon.

the time (i.e. in the geological sense), can the lithophilous percids survive the natural sequence of the aging of their habitats by switching into more advanced guilds? Or are they highly specialized relicts incapable of further adaptation? They may not be given time to supply the answers to these questions.

Responses to Natural and Cultural Succession

Lake metabolism as the selective force — As a river ages it lowers its gradient by erosion. With decreased flow, the lotic environment becomes more and more lentic. The initial transformation from a fluvial into a lacustrine environment is possible in the flood plains of older rivers. Large lakes, fortunately, maintain riverine conditions in their turbulent littoral (Kitchell et al. 1977). The ability to reproduce in increasingly lacustrine environments marks the evolution of percid guilds (Fig. 5).

Consequently, guild sequence may be viewed in some instances as the result of opportunities provided by changes in lake metabolism. The detrital dynamic structures of lakes functionally controls their metabolism (Wetzel 1975). The littoral and autochthonous carbon inputs eventually dominate the syntheses and inputs of organic carbon (Fig. 5). As a result, the littoral flora eventually replaces the pelagic flora as the major driving force in lacustrine systems. As nutrients are added, the contributions of phytoplankton, submersed and emergent macrophytes and attached and eulittoral algae shift with fertility. With increasing nutrient input, succession in the majority of lakes follows the pattern of Fig. 5.

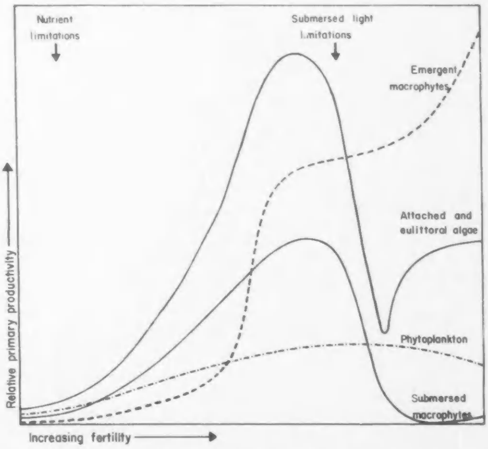

FIG. 5. Generalized scheme of lake metabolism (after Wetzel and Hough 1973 from Wetzel 1975 by permission of W. B. Saunders Co.).

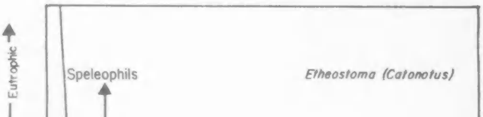
Oligotrophic — LACUSTRINE — Eutrophic
FLUVIAL
Old
Young
Vulnerability
Speleophils
Etheostoma (Catonotus)
Phytophils
Stizostedion lucioperca
GUARDING and NESTING
Perca spp.
Stizostedion marinum
Stizostedion volgense
Phyto-lithophils
Gymnocephalus spp.
Stizostedion vitreum
Lithophils
Stizostedion canadense
Percina spp.
Zingel spp.
Romanichthys sp.

FIG. 4. The vulnerability of guilds and their representative taxa in relation to paleohydrographical sequence of their environment.

The mentioned sequence thus results in replacement of lithophils by phytolithophils and eventually by phytophils. All this can be better demonstrated if an entire fish community is treated (Balon 1975a, b) rather than only percids. Less specialized, nonguarding, open-substrate spawners are in the end replaced by specialized nest spawners and guarders (Fig. 4), but only if lakes become shallower since waves, currents, seiches, etc. tend to keep at least a few rocky areas clear of oxygen-consuming detritus.

Exceptions to the general conditions affecting the detrital dynamic structure in influencing lake metabolism are simply explained in terms of the adjustment of the littoral flora to individual lake conditions. In hardwater lakes, of which marl lakes are an extreme endpoint, dissolved organic carbon interacts with inorganic components such as $CaCO_3$. This normally suppresses carbon metabolism and may lead to pseudooligotrophy. Under conditions of intensive nutrient loading these suppressing mechanisms may be overloaded, promoting rapid transition to highly eutrophic conditions (Wetzel 1972). In softwater lakes, certain macrophytes (e.g. *Sphagnum* sp.) serve as effective ion exchangers with simultaneous release of refractory organic compounds which tend to slow down detrital metabolism and permit the accumulation of organic matter in particulate form (Wetzel and Allen 1970). In hypereutrophic lakes with a large surface area, shallow depth or a large volume, biogenic turbidity severely attenuates light intensity and limits the effect of increasing fertility in producing macrophytic succession.

In percid communities, the replacement of open-substrate-spawning lithophils by phytolithophils and phytophils, and eventually by nest-spawning and guarding phytophils and speleophils, is predictable (Table 1). Thus *Stizostedion vitreum vitreum* would be replaced by *Perca flavescens*; but (if percids interacted among themselves) *S. lucioperca* would not be replaced by *P. fluviatilis*, if such a case existed in nature. However, in natural communities similar interactions occur among salmonids, cyprinids, percids and centrarchids. Even the most advanced percid guild will yield to a centrarchid or ictalurid guild. This is particularly so if the latter belongs to less vulnerable nest guarders or bearers, whose general advantage over open-substrate spawners and even primitive nest guarders is well understood under the K-selection camouflage.

Community structure as a reflection of adaptations to new oxygen and predator–prey regimes — As eutrophication proceeds, the pelagic flora is replaced by the littoral flora with the resulting increase in organic sediment deposition. Adaptations both to lower oxygen regimes and to protection from predators begin to play a more and more important role in community structure.

With the increasing formation of organic substrates the oxygen regime becomes more unstable with oxygen surpluses during the day and oxygen deficits at night. Those species which can oxygenate their eggs in protected situations have a clear advantage over open-substrate spawners. The filling in of the vegetation and the establishment of dense vegetation cover favors nesting species, the vegetation in this case acting as nesting substrate and cover for the young. Again the detrital dynamic structure as affected by nutrient input ensures that certain guilds will be replaced by other guilds, notably open-substrate-spawning phytolithophils by guarding, nest-building phytophils and speleophils.

Many piscivores are open-substrate-spawning lithophils and will collapse suddenly with the mentioned changes, enabling rapid takeover by fishes of the next and better-adapted guild (Chadwick 1976). In other words, the reproductive success of the more advanced guild speeds up extinction of the former guild through reversed predation. This may perhaps have happened with blue pike in Lake Erie. If in addition this is supported by fishing exploitation, which at the same time preys upon the remnants of the failing guild's age groups, replacement of one guild by another can be accelerated.

It follows that lakes in older phases of lake metabolism, exposed longer to the invasion of different fish species, have more diverse fish communities. In a young lake, predation pressure on available spawning grounds is less organized and lower. Hence simple guilds of nonguarding, open-substrate spawners tend to succeed. In highly diverse, old systems chances for survival have to be reinforced by guarding or even bearing of the young (Balon 1975a), and by the extension of spawning grounds into unoccupied areas (Fig. 6). In the large Danube River *S. lucioperca* has to coexist with over 60 other fish taxa; nevertheless, it is in some places very abundant, whereas *S. volgense* is always very rare (Balon 1967b). As would be expected, the guarding and nesting species is clearly more successful. In Quetico Provincial Park (to take this example as a tribute to the PERCIS location), *S. vitreum vitreum* is more widely distributed and coexists with more other species (Crossman 1976) than *S. canadense*. Though the two are members of the same guild, walleye spawns in large aggregations (Regier et al. 1969) whereas sauger does not (Nelson 1968). This difference in reproductive behavior and also

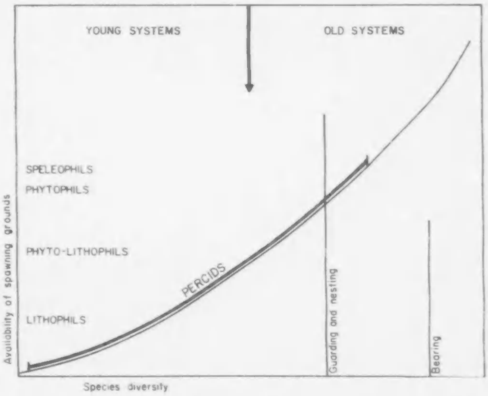

FIG. 6. A simple hypothetical example of percid guilds in competition for spawning grounds and in need for more protection against predators (abscissa).

some of the embryonic adaptations mentioned earlier may be responsible for the success of one over the other. However, none of the North American species of *Stizostedion* live in fish communities as diverse as those in which *S. lucioperca* occurs over most of its range. However, the pike-perch, if it has to live in systems like the Danube or Don river (Khyzhanovsky et al. 1953), maintains a rigid style of guarding and nest building; but in less diverse, northern-like systems, it builds less elaborate nests and its guarding is weak. Are we witnessing the evolution of a new guild?

Guild Response to Catastrophe

For a taxon to switch from one guild to another is a process to be measured in geological time. In certain instances, however, man-made changes can accelerate the process. Normally the adaptations of any given guild make the members strictly limited to a distinctive environment and community structure. Changes in one or both generally mean extinction for the guild. But certain environmental factors are more critical than others, and certain community relationships less detrimental than others. If we concentrate again on the oxygen regime and protection against predation as determinants of guild success or failure, a catastrophe model similar to those constructed previously (Jones and Walters 1976) can be presented. We are, however, not convinced that another erection of such a structure will have the predictive values expected (Peters 1976). May someone follow this lead and prove otherwise?

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Applications of a Bioenergetics Model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*)[1,2]

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A simple energy budget equation is developed to yield a bioenergetics model designed to simulate fish growth. Parameters for the model are estimated from the literature for application to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Simulations are presented that demonstrate model output as functions of body size, activity level, ration level, food quality, and environmental temperature. Sensitivity analyses identify the importance of food consumption, activity, and excretion as biological processes represented in the parameters. On the basis of temperature conditions in selected lakes and specified feeding levels, simulations are presented to quantify the importance of year-to-year variation of temperature in determining growth. In heterothermal systems, temperature selection by percids can have a significant effect on growth. For walleye on fixed rations, annual growth can vary from zero to twofold increments due entirely to differences in summer temperatures. Variations in food quality have lesser effects.

Key words: *Perca*, *Stizostedion*, bioenergetics model, growth, sensitivity, simulations

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Nous formulons une équation simple de budget énergétique conduisant à un modèle bioénergétique conçu pour simuler la croissance des poissons. Nous estimons les paramètres du modèle à partir de la littérature et les appliquons à la perchaude (*Perca flavescens*) et au doré jaune (*Stizostedion vitreum vitreum*). Nous décrivons des simulations démontrant les résultats du modèle comme fonctions de la grosseur du corps, du niveau d'activité, du niveau de ration, de la qualité de la nourriture et de la température ambiante. Des analyses de sensibilité démontrent l'importance de la consommation alimentaire, de l'activité et de l'excrétion comme processus biologiques représentés dans les paramètres. En nous fondant sur les conditions thermiques dans des lacs choisis et à des niveaux d'alimentation spécifiques, nous présentons des simulations permettant de quantifier l'importance des variations d'année en année de la température dans la détermination de la croissance. Dans des systèmes hétérothermes, le choix de la température par les percidés peut avoir un effet important sur la croissance. Chez des dorés jaunes maintenus à des rations fixes, la croissance annuelle peut varier de zéro à des augmentations du double résultant entièrement de différences dans les températures estivales. Les variations dans la qualité de la nourriture ont des effets moindres.

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A model of fish growth gives a better estimation of responses to environment than do population models because growth adjusts biomass more quickly than population density (Kerr 1971; Hall et al. 1970). For percid fishes such as the yellow perch, *Perca flavescens*, and walleye, *Stizostedion vitreum vitreum*, which are tolerant of a wide variety of habit conditions, a model of processes that regulate growth may be used as a sensitive tool in inferring ecological relationships.

A growth model has the capability of integrating a diversity of existing knowledge into a unified framework. This type of modeling has three

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phases. The first step is to mathematically state what is known about the growth-controlling processes that are to be incorporated. This requires a critical evaluation of the results of both laboratory and field studies. Second, the relations of these processes to independent variables must be evaluated. These relations comprise the model hypothesis. If the hypothesis is rigorous, validity of results will depend on validity of the analysis of subprocesses. Finally, the model itself is used as an analytical tool. A sensitivity analysis can indicate what parts of the current understanding of growth require further experimentation. Given a working simulation model, various ecological conditions may be evaluated with respect to their implications for fish growth.

The model described here represents modifications of the bioenergetics components of a population biomass model presented by Kitchell et al. (1974). Consumption and respiration are considered to be the processes that immediately control growth. Temperature and fish size are key variables determining the rates of these processes. Waste losses are modeled as functions of consumption and temperature.

A bioenergetics model hypothesis was chosen as a mechanistic approach to percid biology because it gives a rigorous framework relating the controlling processes to each other, to temperature, and to growth rates. We describe the functions used in the model, our assumptions in their use, and the kinds and sources of data employed as model parameters. We also provide examples of applications that may provide some insights into those factors important to the ecology of percid fishes.

Bioenergetics Approach

The specific growth rate of an individual, nonreproducing fish is calculated as weight increment per unit of weight per time and is defined by the equation

$$\frac{dB}{Bdt} = C - (R + F + U). \qquad (1)$$

Specific growth rate is determined as the difference between specific rate of food consumption, C, and the sum of specific energy output rates, where

R = respiration or metabolism (including standard, active, and specific dynamic action components),
F = egestion,
U = excretion,
and
B = fish weight.

All units are expressed as equivalents in biomass and, for this model, are calculated on a per-day basis. The symbol ΔB is used to represent accomplished growth. Total rates can be calculated as the products of specific rates and fish weights. The following sections briefly describe each of the functions employed in solving Equation 1.

Consumption — The rate of feeding, C, is defined as a function of the maximum rate for an individual fish of a given size at a specified temperature, as follows:

$$C = C_{\max} P r_c \qquad (2)$$

where $C_{\max} = a_1 B^{b_1}$, the maximum weight-specific ration at the optimum temperature, T_o, for consumption; a_1 and b_1 are regression constants,
P = a proportionality constant having values of 0 to 1.0, used to adjust the ration when fitting an observed growth curve,
and $r_c = (V^X)\,(e^{X(1-V)})$, a temperature-dependent proportional adjustment (i.e. 0 to 1.0) of consumption rate.

The function r_c is employed to fit a rate-response curve using three key parameters of biological importance (Kitchell et al. 1974). The slope estimate, Q, approximates a Q_{10} for the rate as it increases with increasing temperature over relatively low temperatures. The value of r_c reaches a maximum of 1.0 at the optimum temperature, T_o, and declines rapidly to zero at the maximum temperature, T_m. Terms for the temperature-dependence function are:

$$V = \frac{T_m - T}{T_m - T_o}$$

$$X = \frac{W^2(1 + (1 + 40/Y)^{1/2})^2}{400}$$

$$W = (\ln Q)(T_m - T_o)$$

$$Y = (\ln Q)(T_m - T_o + 2)$$

and T = ambient temperature.

The allometric function for feeding (and respiration, see below) is a major simplification of the earlier approach to bioenergetics modeling (Kitchell et al. 1974). The allometric consumption function reflects, in part, the change in stomach volume and digestion rates in relation to change in body weight (Brett 1971; Elliott 1976b). Maximum daily rations given by this function are expressed as proportions of fish body weights. This same function is assumed to apply when rations are less than maximum (i.e. $P < 1.0$).

Respiration — The respiration rate is dependent upon body weight and ambient temperature; functions similar to those for consumption are used. In addition, both activity and feeding level affect respiration. Specific respiration, or metabolism, R, is given by

$$R = R_{\max} A r_R + SC \tag{3}$$

where $R_{\max} = a_2 B^{b_2}$, the maximum weight-specific standard respiration rate at the optimum temperature for respiration; a_2 and b_2 are regression constants,

A = an activity parameter to specify respiration rates above standard (i.e. $A = 2.0$ indicates a Winberg II model, Fig. 4b),

$r_R = (V^x)\ (e^{x(1-V)})$, a temperature-dependent proportional adjustment of respiration similar to r_c of equation 2 but with different parameter values Q, T_o, and T_m,

and S = the specific dynamic action coefficient

Values of the allometric function, $R_{\max}$, are expressed as proportions of fish body weights. This reflects the well-known decrease in weight-specific metabolic rate as size increases (Winberg 1956). Specific dynamic action is defined as the metabolic cost of digestion, absorption, and deposition of consumed energy, and is assumed to be a constant proportion of the food consumption rate, C.

Egestion and excretion — Waste losses are defined as egestion, F, and excretion, U. Kitchell et al. (1974) assumed both values to be simple proportions of the feeding rate. A recently published, extensive study by Elliott (1976a) demonstrates that, for the brown trout, both vary as functions of feeding level and temperature. We assume the same to be true for percid fishes and express egestion and excretion rates as

$$F, U = C \alpha T^{\beta} e^{\gamma P} \tag{4}$$

where α, β, and γ are regression constants, and C, T, and P are as defined above. Although the same formulation is used for both rates, the processes respond differently to the variables in Equation 4 as expressed in values for the coefficients α, β, and γ.

Implementing the Model

Two basic data sets are required to implement the model for simulation. Bioenergetics data describe components of the budget equation (Equation 1) as functions of the variables temperature, body size, food quality, and feeding rate (Table 1). Site-specific data are used to provide estimates of ambient temperatures, growth, and food availability. Much of the data employed in parameter estimation for perch was derived from experimental work on *Perca fluviatilis* (Solomon and Brafield 1972) and assumed to be applicable to *Perca flavescens* (Thorpe 1977). Similar data for walleye can be derived from Kelso (1972). Where data were available for one species but not the other, parameter values were assumed to be the same for the two.

The primary components of the model are functions of specified maximum consumption and respiration rates ($C_{\max}$, $R_{\max}$; Equations 2 and 3). We are not aware of direct measures of maximum food consumption rate reported for perch or walleye. Theoretically, the highest rates occur in the smallest free-swimming larvae and these are difficult to study in the laboratory. We estimated the coefficients for $C_{\max}$ using the method of Brett (1971) and extrapolation of data given by Solomon and Brafield (1972), Kelso (1972), and Swenson and Smith (1973). The resultant value of a_1 in Equation 2 was 0.25, so that a 1 g fish would consume a maximum daily ration of 25% of its weight at the optimum temperature. This value is comparable to maximum rations of 24% measured for the bluegill sunfish (McComish 1970) and 30% for sockeye salmon (Brett 1971). Value of the weight exponent, $b_1 = -0.27$, was similarly derived and approximates that reported for largemouth bass, where $b_1 = -0.3$ (Niimi and Beamish 1974).

The standard metabolic rate constant, b_2, was set equal to -0.2, a value typical of many fishes (Winberg 1956). Using basal respiration data for perch of a given weight (Solomon and Brafield 1972) and $b_2 = -0.2$, we extrapolated back to obtain a_2, the value for a 1 g fish. The specific dynamic action, S, component of total respiration was taken as a constant 15% of the food consumed; this is the reported value for both largemouth bass (Beamish 1974) and bluegill sunfish (Schalles and Wissing 1976).

Temperature optima and maxima for consumption and respiration were taken from sources

TABLE 1. Symbols and parameter values used to implement model equations applied to yellow perch (*Perca flavescens*).

Reference equation	Symbol	Parameter description	Parameter value
2	$(C)\ a_1$	Intercept for maximum consumption	0.25
	b_1	Slope for maximum consumption	−0.27
	T_o	Optimum temperature for consumption	
		young-of-year	29°C
		juveniles and adults	23°C
	T_m	Maximum temperature for consumption	
		young-of-year	32°C
		juveniles and adults	28°C
	Q	Slope for temperature dependence of consumption ($\simeq Q_{10}$)	2.3
3	$(R)\ a_2$	Intercept for maximum standard respiration	0.035
	b_2	Slope for maximum standard respiration	—0.20
	T_o	Optimum temperature for standard respiration	
		young-of-year	32°C
		juveniles and adults	28°C
	T_m	Maximum temperature for standard respiration	
		young-of-year	35°C
		juveniles and adults	33°C
	Q	Slope for temperature dependence of standard respiration ($\simeq Q_{10}$)	2.1
	S	Specific dynamic action coefficient	0.15
4	$(F)\ \alpha_1$	Intercept for proportion of consumed food egested	0.158
	β_1	Coefficient for egestion vs. temperature	−0.222
	γ_1	Coefficient for egestion vs. feeding level	0.631
	$(U)\ \alpha_2$	Intercept for proportion of consumed food excreted	0.0292
	β_2	Coefficient for excretion vs. temperature	0.58
	γ_2	Coefficient for excretion vs. feeding level	−0.299

summarized by Hokanson (1977). Optimum temperatures for consumption and growth of yellow perch are about 23°C (Schneider 1973), and this is equal to the average final laboratory temperature preferendum for this species (Neill and Magnuson 1974). Close correspondence between temperature preference and the optima for activity and growth is known for other fishes (Brett 1956). The ultimate upper incipient lethal temperature was used as maximum temperature for respiration and it sets the upper bounds on the system. The difference between T_o for consumption and T_m for respiration is 10°C; the midpoint between these, 28°C for adult perch, was arbitrarily chosen as both T_m for consumption and T_o for respiration. This is essentially equal to the maximum observed temperature preference for yellow perch (i.e. 29°C, lab; 27°C, field; Hokanson 1977). Values for Q were taken from Kitchell et al. (1974).

Elliott's (1976a) equations for egestion and excretion rates in brown trout as functions of temperature and ration were assumed to be applicable to percids. The partial regression coefficients β and γ were taken directly from Elliott and the intercepts α_1 and α_2 were adjusted to fit the curves through Solomon and Brafield's (1972) F and U estimates for *P. fluviatilis* eating *Gammarus* sp. at 14°C. The proportion of ingested food that is egested at $C_{\max}$ and 14°C is conveniently about equal to the value of α_1. Thus we set α_1 to the approximate known egestion values for each food type at 14°C (see Table 2 and related text).

Model Applications

Environmental temperatures constitute a major determinant of growth under specified feeding regimes. Unfortunately, many extensive field studies of growth, population dynamics, and production have not included or reported temperature data. Our applications of the model are restricted to those sites where water temperature data have been reported. An adequate simulated profile of surface water may be derived from four known parameters: average date of ice disappearance, date and values for maximum midsummer temperature, and average day of first complete ice cover. With this information, the temperature curve for the ice-free period can be simulated using a skewed sine function. Actual daily temperatures or interval data with linear interpolation between observations can be used for the model. In these simulations we employ data from Lake Erie (Jobes 1952; Burns 1976) and Oneida Lake (Forney 1977). Using reported growth rates, we used the model to evaluate hypotheses regarding fish growth in these systems.

We used the parameters described in the preceding section and summarized in Table 1 to perform simulations that demonstrate model outputs (Fig. 1–5) as functions of the variables temperature, body size, activity, and ration level.

For a 10 g yellow perch feeding at maximum levels, all components of the energy budget equation are expressed as functions of temperature (Fig. 1). Maximum growth rate occurs at about 22°C, and growth declines rapidly between 22 and 28°C. The relationship of growth and temperature as shown here agrees closely with that observed by McCormick (1976) for juvenile yellow perch. Starvation is assumed to be represented by standard respiration rates at temperatures greater than 28°C; this provides a conservative estimate of weight loss during starvation since excretory and other losses are not simulated.

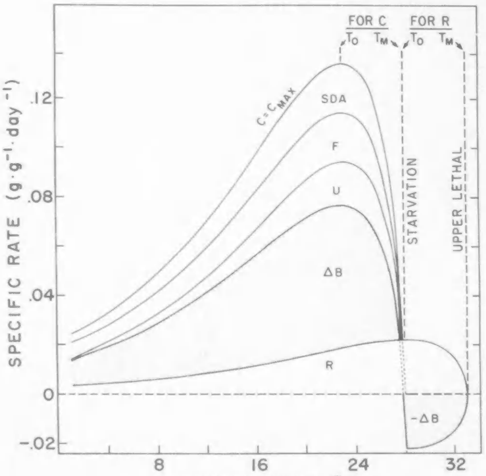

FIG. 1. Model output of the relations between temperature and all component rates of the energy budget for a 10 g yellow perch. Symbols are those given in Equation 1. Parameters are those summarized in Table 1.

Changes in weight-specific rates for energy budgets at maximum rations are displayed as a function of fish weight to demonstrate the allometric effect (Fig. 2). Optimum temperature for consumption was set at 23°C and for respiration at 28°C. All rates decline rapidly over the 1–50 g size range and more slowly for fish greater than 50 g. Small fish have a greater scope for growth than large fish because the C and R functions converge with increasing size (i.e. $|b_1| > |b_2|$).

Egestion and excretion of invertebrate (e.g. *Gammarus*) foods vary as a function of temperature and ration level. At maximum rations ($P = 1.0$), the proportion egested declines as temperature increases while that excreted increases with rising temperature (Fig. 3). The cumulative net loss as waste varies only slightly (26–32%) with more than 30% lost at very low and high temperatures. Maximum absorption efficiency would occur at high temperatures but would be offset by a relatively high excretory loss. Hence, the temperature range of 4 to 12°C appears most efficient for growth at minimum waste loss rates. Both loss rates are altered by consumption levels less than maximum to yield increased efficiency at reduced rations.

We combined all functions to simulate the effect of temperature on estimated maintenance rations for fish of 1 g to 1 kg (Fig. 4a). Maintenance rations are inversely related to body size as suggested by the simulations of allometric effects (Fig. 2). They are highest at about 27°C

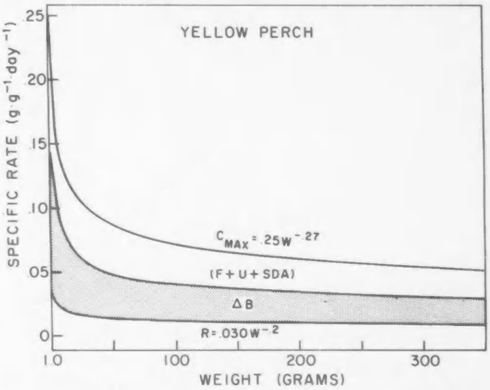

FIG. 2. Relations between body size and components of the energy budget for yellow perch at 23°C. Allometric functions for maximum consumption and respiration rates are from Equations 2 and 3.

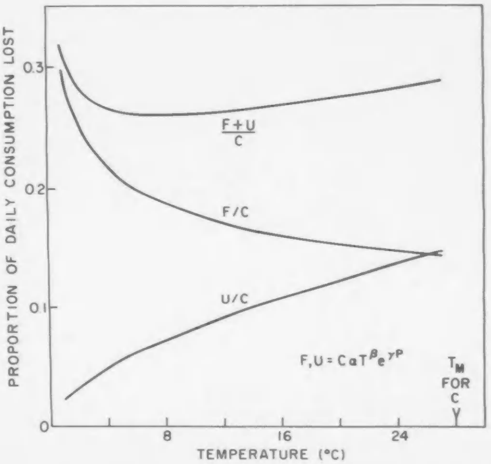

FIG. 3. Proportions of consumed food egested and excreted and their sums as functions of temperature. Calculated values are based on Equation 4.

for all sizes, being greater than 6% of body weight for a 1 g fish and about 1.5% for a 1 kg fish. Maintenance rations at low temperatures (<4°C) would be about 1% and 0.2% for 1 g and 1 kg fish, respectively. The inference of reduced maintenance rations at temperatures greater than 27°C reflects the decline in feeding rates observed at high temperatures and the resultant reduction in losses to egestion, excretion, and specific dynamic action (Fig. 1).

Ware (1975) discusses the continuing controversy regarding estimates of activity and metabolic levels ascribed to free-living fishes. Winberg (1956) proposed that the level of laboratory-determined standard metabolism (Winberg I) be doubled (Winberg II) in estimating respiratory energy utilized by fishes in nature. Many subsequent studies have applied this procedure as a rule of thumb (Mann 1969). Ware (1975) proposed that pelagic, juvenile fishes had activity levels equivalent to Winberg III.

To assess the bioenergetics of variable activity, we simulated growth rates at each of three activity levels as a function of temperature (Fig. 4b) for a 10 g yellow perch consuming maximum rations. At high activity levels (III), maximum specific growth rate (~2% day^{-1}) occurs at about 20°C. At low activity levels, those we assume to be equivalent to standard respiration rates (I), maximum growth is nearly 6% at 23°C. The optimum temperature for maximum specific growth rate declines slightly as activity levels increase. With the exception of results given in Fig. 4b, all simulations presented herein assume a Winberg I model ($A = 1.0$).

We specified fixed ration levels in simulations of growth by a 10 g yellow perch at various temperatures. Rations were set equal to $C_{\max}$ at temperatures where specified rations exceeded $C_{\max}$. The results are expressed as specific growth rates for rations of 1% of body weight to maximum (13%) (Fig. 5a). Growth rate declines

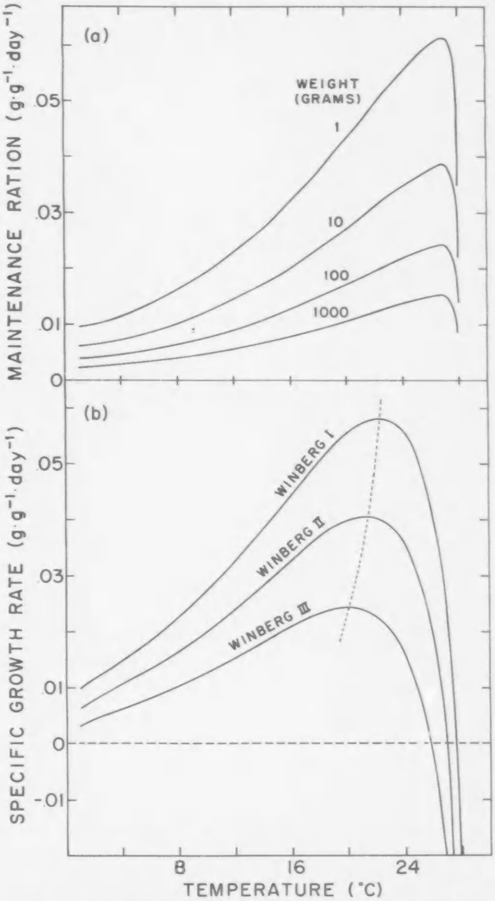

FIG. 4. (a) Relations between temperature and estimated maintenance rations for perch of four weights when maintenance $= R/1.0 - (F/C) - (U/C) - S)$. Adult temperature parameters were used for the 1 g fish to facilitate comparison. (b) Specific growth rates at maximum rations for a 10 g perch as functions of temperature and multiples of the standard respiration rate used to estimate levels of activity in nature.

with increasing temperature at all ration levels. The zero growth line in Fig. 5a represents maintenance rations as a function of temperature ranging from 1% at 8°C to nearly 4% at 27°C.

We calculated and plotted gross and net conversion efficiency isopleths for the specified ration levels. Gross conversion efficiency (Fig. 5b) exceeds 45% at the highest rations obtained over the 4–20°C temperature range. Net conversion efficiencies (Fig. 5c) exceed 64% at low ration levels and temperatures less than about 10°C. Net efficiencies are lowest (<58%) at high ration levels and high temperatures.

Elliot (1976b) found that highest gross conversion efficiency for brown trout also occurred at maximum rations and intermediate temperatures. Our simulation results and Elliot's laboratory observations both contrast with the observation that fingerling sockeye salmon have maximum gross conversion efficiency at ration levels less than maximum (Brett et al. 1969). The data of Brett et al. indicate a reduction in assimilation efficiency as ration approaches the maximum for a given temperature. Brown trout also have lower assimilation at high rations (Elliot 1976a) but still have highest gross conversion efficiency at maximum rations and intermediate temperatures.

The difference between Elliot's (1976b) results and those of Brett et al. (1969) may be due, in part, to differences in their experimental designs. Elliot fed natural foods to individual fish whereas Brett et al. fed a pellet diet to a large group of fish and periodically subsampled the group to determine growth. Since Brett et al. did not recover and quantify uneaten food in all experiments, it is possible that they progressively overestimated the actual quantities consumed by a tank population when rations approached the maximum for a given temperature. It is also possible that the assimilation efficiency of sockeye salmon eating pellet diets is somewhat different from that of brown trout eating natural foods.

Sensitivity Analysis

Methods and assumptions — A single parameter analysis of sensitivity was done to evaluate the relative importance of input parameters for yearly growth output. We simulated growth of age I+

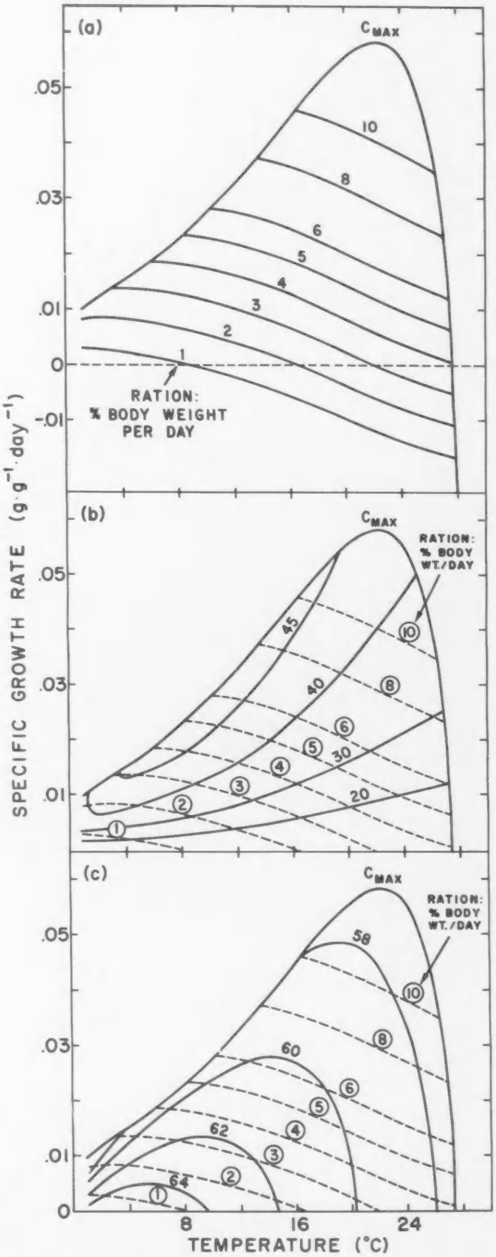

FIG. 5. (a) Specific growth rates for a 10 g perch as functions of temperature and specified ration levels ranging from 1% of body weight to maximum. (b) Relations between gross conversion efficiency (isopleths, %) and temperature for a 10 g perch when gross efficiency (%) = $(\Delta B/C) \times 100$. Isopleths (solid lines) are plotted from simulations at those specified ration levels represented by broken lines. (c) Relations between net growth efficiency (isopleths, %) and temperature as described for Fig. 5b when net efficiency (%) = $[\Delta B/(C - \text{Maintenance})] \times 100$.

yellow perch in western Lake Erie using the parameter values for adult fish in Tables 1 and 3 as nominal values. The simulation used a temperature curve (Fig. 8b) derived from observed temperatures in western Lake Erie. We assumed that perch orient to their preferred temperature, and that water of this temperature was available throughout the summer although surface temperatures higher than preferred were observed. Under these conditions simulated growth of a yearling perch with a starting weight of 9 g was 51 g in 1 yr for a final weight of 60 g.

Each parameter was separately varied ±10% and the simulation rerun. Temperature inputs, such as optimum temperature for consumption (T_o) and preferred temperature (T_p), were varied ±1 deg. C.

The model sensitivity of yearly growth for each parameter is

$$s(p) = \frac{p \cdot \Delta(\Delta B)}{\Delta B \cdot \Delta p},$$

where $s(p)$ = yearly growth sensitivity for p,
p = nominal value of parameter p (Table 1),
Δp = input deviation of parameter p,
ΔB = nominal yearly growth ($B_1 - B_o$),
$\Delta(\Delta B)$ = change in simulated yearly growth due to Δp,
B_o = weight at beginning of year,
and B_1 = weight at end of year.

Since $p = 10 \cdot \Delta p$ (except for temperature parameters), sensitivities for parameters were calculated by

$$s(p) = \frac{10 \cdot \Delta(\Delta B)}{\Delta B}$$

A sensitivity of $s(p) = \pm 1.0$ means that a change of parameter p by 10% causes a resultant 10% change in simulated yearly growth. Sensitivities of $|s(p)| > 1.0$ indicate higher sensitivities of simulated growth to p; values of $|s(p)| < 1.0$ indicate lower sensitivities. For example, $s(p) = -0.5$ means that, for a 10% change (or error of estimate) of input parameter p, simulated yearly growth decreased by 5%.

Results and conclusions — Results of the sensitivity analysis (Fig. 6) can be interpreted with respect to both the internal operation of the modeling equations and the intrinsic function of each parameter. Analysis of internal operation is of most utility in evaluating the degree of success with which the model simulates the intended bioenergetic relationships. As such, this type of analysis is most useful to the modeler and is discussed only briefly. A second use of the sensitivity analysis is to assess the importance of the relations between the biological meaning of each parameter and the output, yearly fish growth.

The sensitivities calculated are self-normalizing and give a good measure of the relative importance of each parameter to simulated annual fish growth (Fig. 6). These results are strictly applicable only to the specific simulation analyzed. For conditions of other lakes, year-classes, and growth assumptions, the results may be considerably different. For instance, the model sensitivities for changes of 1 deg. C in maximum temperatures of respiration and consumption are low for the Lake Erie simulations, but might be very high for systems with higher summer temperatures.

We emphasize that this analysis is done for yearly growth sensitivity. If yearly growth is known and the model is used to estimate consumption, sensitivities of consumption output to errors of parameter estimates would be much lower. Preliminary results indicate that estimation of consumption in this manner provides accurate output despite relatively large uncertainties in the values of nonconsumption related parameters. We consider that the model will be a powerful tool for evaluating predator–prey systems.

For the simulations performed, parameters with highest overall sensitivity are P and a_1. Although they operate identically in the model, each has a different meaning. The parameter a_1 defines the amount of food a perch can eat; P is the proportion of a_1 that a perch actually eats. High sensitivities of P and a_1 do not adversely affect the operation of the model as it was used for simulations presented below, since P is the parameter

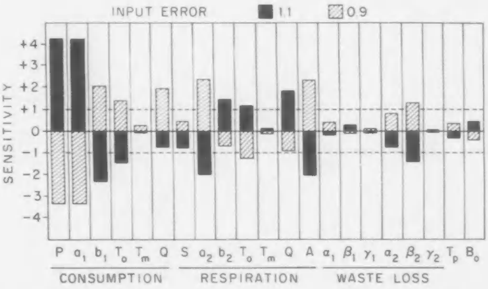

FIG. 6. Normalized sensitivities to 10% changes (1.1 × or 0.9 × nominal value) of each parameter used to simulate yearly growth for age I+ yellow perch in the western basin of Lake Erie. In addition to the parameters given in Table 1, others are defined in the equation series and text.

used to fit observed growth. The sensitive respiration parameters a_2 and A have the same operational relation to each other as do a_1 and P. The assymetry of both Q sensitivities stems from the extreme nonlinearity of the temperature dependence of both respiration and consumption.

Sensitivity of the model to errors in the estimate of different parameters varies considerably. The degree to which these sensitivities represent uncertainty in estimation of yearly fish growth is related to how well the phenomenon represented by the parameter is known. For example, growth is highly sensitive to errors in A, the level of in situ metabolism, which is poorly known. Refinement of the lethal temperature parameter (T_m for respiration), which is well known and has a low sensitivity, would not contribute substantially to our present understanding of the growth process.

New research is most needed on those relationships which are most critical to fish growth (high sensitivity) and which are least well known. We attempt to identify areas of greatest need for research using these considerations. The availability of estimates for a given parameter is a complex function of the adequacy and frequency of measurement. Parameter sensitivities and our subjective judgments of the availability of estimates are classified as high, moderate, or low. The need for further research was judged by the following algorithm:

	Availability of Estimate		
Sensitivity	*High*	*Moderate*	*Low*
High	Moderate	High	High
Moderate	Low	Moderate	High
Low	Low	Low	Moderate

The results of this exercise are presented in Table 2. We conclude that the highest priority for percid research should be to determine the allometric specific rate functions (aB^{-b}) for maximum consumption and routine metabolism. These rates are highest in young-of-the-year fishes and the first year-class contributes a high proportion of the total production in many systems (e.g. Chadwick 1976). Estimates of the metabolic cost of daily activity ($\sim A$) in the field are difficult to make but might be worth pursuing as such measures might contribute importantly to our knowledge of ecological bioenergetics. The moderate sensitivity of excretion parameters was an unexpected result. Waste losses have been adequately evaluated for only one fish species, the brown trout (Elliot 1976a). Comparable studies on percids and other fishes may be useful.

TABLE 2. Summary of sensitivity analysis of model parameters and implications of need for further research. Qualitative evaluations are given as high (H), moderate (M), or low (L). Parameter symbols are those given in Table 1 and the text.

Parameter	Sensitivity	Availability of estimate	Need for further research
Consumption			
a_1	H	L[a,b]	H
b_1	H	M[a]	H
P	H	L[b,c]	H
T_o	M	H	L
T_m	L	L[a]	M
Q	M	M	M
Respiration			
A	H	L[b,c]	H
a_2	H	M[a]	H
b_2	M	M[a]	M
T_o	M	H	L
T_m	L	H	L
Q	M	H	L
S	M	M[a,b]	M
Waste Losses			
α_1	L	L[a]	M
β_1	L	L[a]	M
γ_1	L	L[a]	M
α_2	M	L[a]	H
β_2	M	L[a]	H
γ_2	L	L[a]	M
T_p	L	H	L
B_o	L	H	L

[a] Known for other species; derived by extrapolation of available yellow perch data.

[b] Measured in laboratory; poorly known and variable under natural conditions.

[c] Specified for simulations.

Simulated Growth of Lake Erie Yellow Perch

Applications of the model to available data are presented in this section and in the following two sections. Assumptions made are given as hypotheses and the simulation results should be viewed as such. Although many applications are possible, those presented are best viewed as examples chosen to demonstrate various components of the model.

Methods and assumptions — We conducted two simulations of yellow perch growth in Lake Erie (Fig. 7). In the first simulation, growth data presented by Jobes (1952) were fitted with the model using parameter values given in Tables 1 and 3 together with a water-temperature curve (Fig. 8b) for the western basin of the lake. Weight of fish at annulus formation was based on Jobes' data pooled for both sexes. For the second

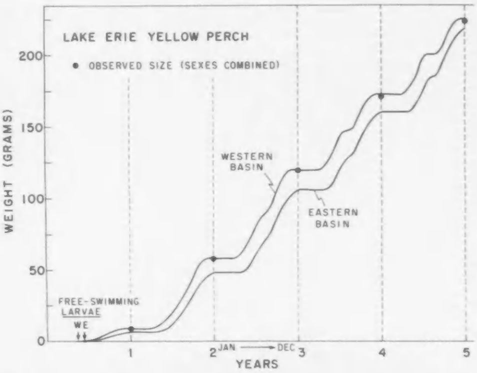

FIG. 7. Simulated growth of yellow perch under the thermal conditions of western and eastern Lake Erie. Observed growth data are from Jobes (1952); parameter values, from Tables 1 and 2; annual temperature data (Fig. 8b), from Burns (1976).

simulation, we used a water-temperature curve (Fig. 8b) for the extreme eastern end of Lake Erie; all other parameters were the same as in the first simulation. The eastern end of Lake Erie has an annual thermal cycle approximately one month behind that of the western basin (Burns 1976). Maximum summer temperatures of 23°C in the eastern basin were lower than those (24°C) recorded for the western basin during 1970. We assumed homothermous conditions in both areas of the lake.

Temperature optima and maxima for consumption and respiration rates of young-of-the-year fish were used for first-year growth. All other age-classes were assumed to be physiologically adult (Table 1). Young-of-the-year fish were assumed to prey exclusively on invertebrates. For the second year of growth the diet was assumed to be 50% invertebrates and 50% fishes. All older fish were assumed to be exclusively piscivorous. Values of α_1 for egestion were varied from 0.158 for invertebrates (Solomon and Brafield 1972) to 0.05 for fish prey (Kelso 1972) to estimate changes in food quality.

To begin the growth simulations, we assumed that spawning was initiated by spring water temperatures of 11°C (Hokanson 1977), that hatching required 10 days, and that larvae were free swimming (weighing 0.04 g) 5 days after hatching. Simulations of growth were, therefore, begun 15 days after 11°C was first determined in the annual thermal cycle. During winter months, consumption was assumed to be equivalent to maintenance rations; therefore, no growth occurs at temperatures $\leqslant 2.0$ C (Fig. 7). Values for P (Equation 2, Table 3) were adjusted for each year-class to yield the simulation results given in Fig. 7. Values for P approximate the ratio of the maximum potential and estimated (or realized) daily rates of food consumption.

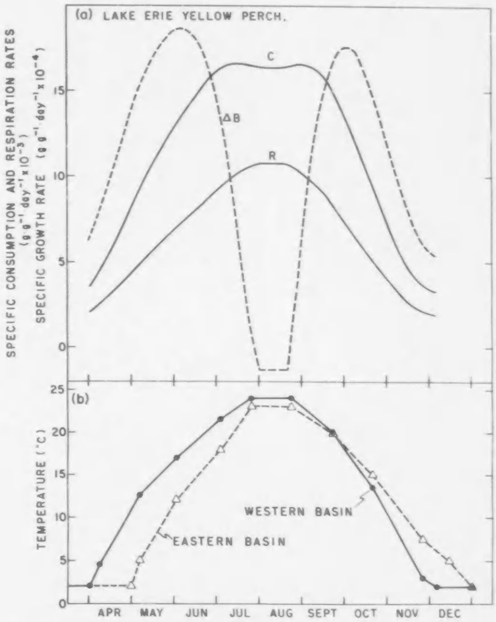

FIG. 8. (a) Simulated specific rates of food consumption, respiration, and growth for age IV+ yellow perch in western Lake Erie. (b) Cycles of surface water temperature for western (83°, W L.) and eastern (79°, W L.) Lake Erie during 1970. Data are from Burns (1976) with linear interpolations between observations.

TABLE 3. Weight data and parameter values used to simulate growth of yellow perch in Lake Erie.

Age-class	Weight (g) at annulus formation	α_1 for egestion	P for consumption
I	9	0.158	.522
II	58	0.100	.378
III	119	0.050	.309
IV	172	0.050	.284
V	224	0.050	.279

Results and conclusions — Simulation results for the thermal regime of western Lake Erie yield a virtually linear growth response for juvenile perch during those times of the year when growth occurs. For older, larger perch, growth is rapid during spring, slows or ceases during midsummer and resumes during fall months. Simulated growth of young-of-the-year perch suggests food consumption rates approximately one-half the estimated maxima ($P = 0.522$). Values for P decrease with age, implying an increasingly severe food limitation.

We determined specific rates of respiration, food consumption, and growth during the fifth year of growth (Fig. 8a). Although maintenance rations are lower for larger fish (Fig. 4), the allometric relations of food consumption and respiration rates make growth of larger fish markedly reduced by high midsummer temperatures. A distinctly bi-modal growth response emerges as size increases. Kitchell et al. (1974) discussed a similar bi-modal growth pattern observed in adults of many fish species. Also, see Forney (1977) on Oneida Lake walleye.

Respiration rates given in Fig. 8a generally reflect correspondence with existing water temperature. Consumption also parallels thermal conditions except during midsummer months, when the rates are nearly constant. As a result, the net energy available for growth is substantially reduced and a negative energy budget arises for maximum temperature conditions during August. A strongly bi-modal growth pattern results with growth during spring being greater than that during fall due to the allometric relations proposed for consumption and respiration.

Simulated growth of perch under the thermal regime of eastern Lake Erie (Fig. 7) emphasizes the thermal effect. Perch in the eastern basin are smaller at a given age than those in the western basin due to: (1) delayed hatching (assumed for the simulation) resulting in a reduced growing season during the first year and a smaller initial size for each subsequent year, and (2) reduced growth rates for young-of-the-year and juveniles (age I+) due to the lower thermal regime. For older fish, the differences are reduced; growth in the eastern basin shows less midsummer reduction, reflecting the lower maximum temperature.

Simulated Growth of Oneida Lake Walleye

Methods and assumptions — To evaluate applications of the model to walleye and to short-term growth data, we simulated growth of age III+ fish in Oneida Lake (Forney 1977) during that period of the year when growth occurred (May–September). Parameters given in Table 1 were assumed applicable to walleye except that thermal optima and maxima were reduced 1 deg. C for respiration and consumption; e.g. $T_o = 22°C$, $T_m = 27°C$ for C; and $T_0 = 27°C$, $T_m = 32°C$ for R (Koenst and Smith 1976; Hokanson 1977). Assuming a 240-day ice-free period, a maximum midsummer temperature of 24°C, and an initial weight of 280 g, a value for $P = 0.4425$ yielded a final weight of 517 g, which is equivalent to that observed.

Using 27°C (Forney 1977) as the midsummer maximum, we also simulated walleye growth employing the same parameters as those for the 24°C simulation. Lastly, we assumed that walleye would behaviorally thermoregulate during midsummer, maintaining themselves in 22°C water when surface water temperatures exceeded 22°C during a cycle with a maximum of 27°C.

Results and conclusions — Although the 24°C simulation (Fig. 9) was fitted to the initial and final weights, the simulated growth underestimates the observed. The 22°C simulation, in which behavioral thermoregulation was assumed, more closely corresponds to the growth data for midsummer through late summer. High temperatures of the 27°C simulation result in weight loss during midsummer. Although growth occurs in spring and fall, net change in weight is negative under the ration levels specified.

It is important to note that all three simulations assume that only temperatures and body size determine ration levels. That condition is specified in a constant value of P. Intraseasonal changes

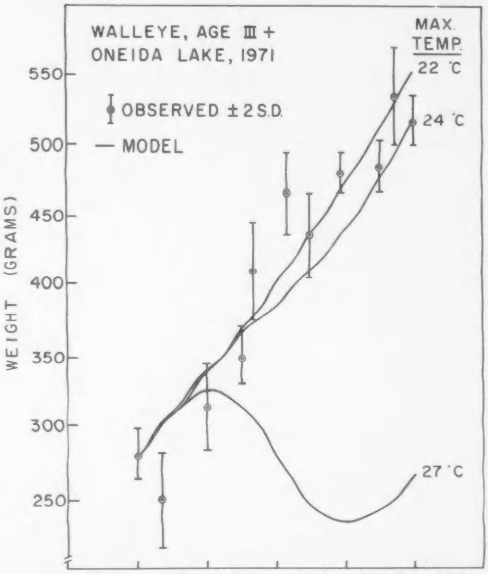

FIG. 9. Simulated and observed growth of age III+ walleye in Oneida Lake during 1971. Observed data are from Forney (1977). See text for explanation of assumptions regarding maximum summer temperatures. Water temperature during the ice-free period was simulated with a skewed sine function.

in food availability are not simulated. The observed data undoubtedly represent greater variation in actual feeding rates than that assumed by the simulations. However, the assumption of equivalent rations points to the very significant effect on growth rates of year-to-year and seasonal variation in temperature. Within the observed range, differences of only a few degrees in maximum summer temperatures can have marked effect on annual growth. Access to temperatures optimal for growth and behavioral thermoregulation in heterothermal environments may yield growth rates substantially different from those expected from the assumption of random distribution throughout the epilimnion.

Effects of food quality — To assess the relative importance of prey quality we varied the value of the egestion constant, α_1, to represent an all-fish diet ($\alpha_1 = .05$), an all-invertegrate diet ($\alpha_1 = .15$) and a mixed diet ($\alpha_1 = .10$). Each was simulated under the three thermal regimes and parameter values used for Oneida Lake. We assumed the energy cost of predation to be the same for all prey types.

Variations in food quality under a given thermal regime result in relatively small differences in total growth (Table 4). Given the same prey, thermal conditions can account for substantially greater differences in growth. The optimal condition of piscivory and thermoregulation results in fish twice the final size of those grown under conditions of an all-invertebrate diet with high midsummer temperatures.

TABLE 4. Simulated final weights (g on day 269, October 1) of age III+ walleye in Oneida Lake, New York, as functions of varied thermal conditions and prey type. Initial fish weight was 280 g on May 30 (day 150). See text for details of assumed conditions of each simulation.

Maximum Temperatures	Proportion egested (α_1) .05	.10	.15
24°C	517	479	443
27°C	265	250	235
22°C	551	509	470

Comparative Growth Responses

Although our model does not explicitly allow for competitive interactions, a simple comparative growth response under equivalent environmental conditions can provide some insights regarding competition between percids and sympatric fishes optimally adapted to other thermal regimes.

Methods and assumptions — For simulation of these relations we used a hypothetical cold-water or salmon-like fish having 15°C as T_o for consumption and 19°C as T_o for respiration. Temperature maxima for the salmonid were 19°C for C and 23°C for R. For a hypothetical warmwater or centrarchid-like fish, we used thermal parameters given by Kitchell et al. (1974) for bluegills: $T_o = 27$, $T_m = 31$ for C; $T_o = 30$, $T_m = 34$ for R. All other parameters and those for a percid fish were taken from Table 1. Growth was simulated using the annual thermal regime (Fig. 8b) of western Lake Erie; an initial weight of 100 g was assumed and April 1 was designated as the beginning of the growing season. Two feeding levels were simulated with $P = 0.38$ or 0.25 for all three fish types (Fig. 10).

Results and conclusions — For the lower ration level, the warmwater or centrarchid-like fish appeared to be at maintenance rations throughout the April through December simulation period. The salmonid-like fish grew slightly in spring but lost weight during the warm summer months. The percid fish grew during spring and fall to a final weight of 119 g. At the higher rations levels, all three fish grew. However, the salmonid lost weight during periods of high temperature. Both the centrarchid and percid fish grew throughout the simulation period.

Three important conclusions arise from the simulation results. 1) In years when rations are relatively low, the seemingly slight growth advantage of the percid fish becomes cumulative. Assuming a parallel of growth, other components of fitness, and, ultimately, competitive superiority,

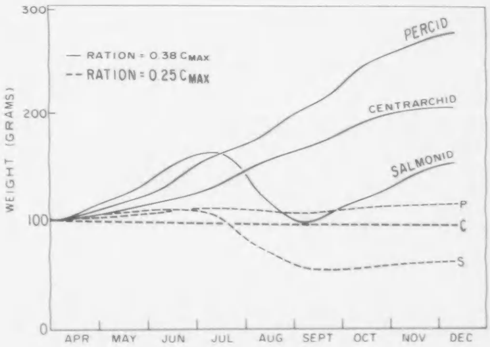

FIG. 10. Simulated growth at two ration levels for hypothetical warmwater, coldwater, and percid fishes in the western basin of Lake Erie.

slight differences in growth during any single year may ultimately result in dominance by one form over its competitors. 2) To accomplish annual growth equivalent to that of a percid in Lake Erie, the coldwater and warmwater fishes must consume substantially higher rations. 3) The most successful fishes in a homothermous system such as the western basin of Lake Erie are probably those with maximum growth rates at or about the maximum observed temperature.

These generalizations are most applicable to homothermous systems. As concluded from the Oneida Lake simulation, growth responses in a thermally stratified lake might be noticeably different. In heterothermous lake systems, the maximum growing season for a species may be at the southern limits of its range. These lakes provide near optimum water temperatures at some depth for the longest part of the year even though surface waters may become warm enough to retard growth. The largest individuals of any given species should be found near the periphery of the range dictated by high temperatures. This seems to be true for yellow perch and walleye (Scott and Crossman 1973).

General Discussion

As proposed, the model is best applied in attempts to evaluate growth responses of an average or typical member of the population under the average of environmental conditions. Implementation of reproduction and mortality functions allows simulations of the entire population. A known growth curve, a record of thermal experience during the observed period, plus estimates of feeding rates and prey types are the site-specific data sets neded for adequate applications of the model. Known components may be used to simulate an unknown. For instance, growth and temperature data are sufficient to estimate consumption and, hence, effect of a predator on its prey. Growth data are most readily available, complete thermal records and food habits studies less so, and measures of feeding rates scarce. The variation in growth which we hypothesize may be due to variation in temperature alone (Fig. 9) suggests that regular temperature measurement should become an integral part of future population and growth studies. Food habits studies have greatest value when employed in determining rates of feeding (Table 4, Fig. 5a).

The model is sufficiently general for application to a wide variety of fishes. To fully implement the energy budget model as conceived, critical data sets required for a given species include respiration and maximum consumption rates as functions of body size and temperature, plus egestion and excretion as functions of temperature and ration levels. These functions provide the boundaries to the scope for growth. Each species may have its characteristic bioenergetic boundaries, and once these are determined a greater understanding of the distributional and behavioral ecology of the species may be attained. Except for the excellent studies on salmonids (Brett et al. 1969; Elliot 1976b), bioenergetics data at temperatures near the upper and lower tolerance levels of most fishes are generally lacking. Also, a need exists for research on the bioenergetics of young-of-the-year fish.

The process of parameter determination would clearly be facilitated by an abundance of experimental data. Unfortunately, such data for percids are not available for many of the parameters in the equation series. Where data are lacking, we can only extrapolate from existing information and use the resultant formulation as an untested hypothesis. All parameters employed in our model may be directly measured; the extrapolations and assumptions are open to rigorous experimental evaluation.

Acknowledgments

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Percid Habitat: The River Analogy[1]

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We propose that the optimum habitat of the percid fishes *Perca flavescens*, *P. fluviatilis*, *Stizostedion vitreum vitreum*, and *S. lucioperca* in lakes may be defined by the littoral and sublittoral environmental conditions equivalent to those in large, temperate rivers. Analogous habitat conditions include sand or gravel substrate, low current velocity, reduced light penetration (*Stizostedion* spp. only), temperatures optimal for growth and reproduction, and well-oxygenated spawning substrates. The species' evolutionary origins and reproductive patterns also reflect their riverine ancestral habitat. Evidence in support of the hypothesis is derived from the diversity of papers contributed to the PERCIS Symposium.

Key words: Percidae, habitat, theory, *Perca*, *Stizostedion*

KITCHELL, J. F., M. G. JOHNSON, C. K. MINNS, K. H. LOFTUS, L. GREIG, AND C. H. OLVER. 1977. Percid habitat: The river analogy. J. Fish. Res. Board Can. 34: 1936–1940.

Nous suggérons que l'habitat optimal des percidés *Perca flavescens*, *P. fluviatilis*, *Stizostedion vitreum vitreum* et *S. lucioperca* dans les lacs soit défini par des conditions de milieu littoral et sublittoral équivalentes à celles des grandes rivières tempérées. Les conditions analogues du milieu incluent: substrat de sable ou de gravier, faible vitesse de courant, pénétration lumineuse réduite (*Stizostedion* spp. seulement), températures optimales de croisssance et de reproduction, et substrats bien oxygénés pour la fraie. Les origines des espèces et les modalités de la reproduction reflètent également leur habitat ancestral fluviatile. Les preuves à l'appui de cette hypothèse sont extraites des divers articles soumis au colloque PERCIS.

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ON the basis of the Colby et al. (1972) prototype of habitat description, a percid habitat may be best defined by comparison of environmental conditions within a spatial or temporal continuum. The primary objective of this paper is to present a hypothesis that allows more appropriate identification of percid habitat in lakes. We confine our treatment to two economically important percids of North America, the yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*), and their European counterparts, the Eurasian perch (*P. fluviatilis*) and pikeperch (*S. lucioperca*).

Perca spp. and *Stizostedion* spp. occur in rivers and lakes ranging from oligotrophic to eutrophic,

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and are often sympatric components of salmonid or centrarchid–cyprinid dominated communities. They occur over a broad geographic region having temperate climates. In simple terms, they are in the middles of both the north–south climatic and geographic gradients and for lakes within that zone, may persist throughout the temporal progression of cultural eutrophication. As eutrophication proceeds within a given lake, the optimum habitat first expands and then constricts.

Few universal criteria apply to all percid habitats. In Table 1 we present criteria that commonly define presence or absence of *Perca* spp. and *Stizostedion* spp. and those that characterize systems with well-developed percid populations. To broadly summarize our view of the percid habitat, we present a series of graphic relationships depicting variable geographic and/or temporal gradients scaled in relation to optimal habitat conditions (Fig. 1). Empirical data are presented where limiting conditions are known (Table 1).

An obvious difference exists between North American percids and their European equivalents. The latter appear much more tolerant of eutrophication and high-temperature conditions (Thorpe 1977; Weatherly 1977; Hokanson 1977). *S. lucioperca*, in particular, has evolved parental care of eggs as a reproductive behavior allowing its persistence in more eutrophic systems (Fig. 1) (Collette et al. 1977; Marshall 1977). Other habitat requirements and various histories of responses to environmental changes are presented in this issue (e.g. Collette et al. 1977; Johnson et al. 1977; Kerr and Ryder 1977).

With regard to the conditions outlined in Table 1, we sought to specify the North American habitats of *P. flavescens* and *S. vitreum vitreum* within the group of Ontario lakes described by Leach et al. (1977). A consideration of all lakes yielded few generalizations. *Perca flavescens* is broadly distributed and *S. vitreum vitreum* somewhat less so. A major contradiction appeared in that *S. vitreum vitreum* is present in many small lakes (<100 ha) but abundant in only some. All the criteria of Table 1 also apply to temperature-zone rivers. By hypothesizing that those small lakes where *S. vitreum vitreum* was abundant were components of a drainage system, i.e. components of a larger system connected by a river, we could explain most of the anomalous observations of *S. vitreum vitreum* occurrence and abundance in small lakes.

TABLE 1. Selected criteria of optimum habitat for *Perca* spp. and *Stizostedion* spp.

Variable	Attribute
Lake bathymetry	Shallow–moderately deep
Lake morphometry	Extensive littoral and shoreline area
Substrate	Sand-large gravel, submerged vegetation
Lake size	>100 ha (*Stizostedion* spp. only)
Light penetration	Secchi <2 m (*Stizostedion* spp. only)
Temp optimum for growth	
juveniles	<27–31°C
adults	<22–26°C
Temp optimum for gonad maturation	<12°C during winter
Min O_2 at spawning substrate	$>2\text{–}4\ \mathrm{mg}\cdot\ell^{-1}$

The River Analogy

We propose that the habitats of *Perca* spp. and *Stizostedion* spp. in lakes may best be identified by conditions analogous to those in temperate rivers. Most North American and European lakes are of recent origin, the result of Pleistocene glaciation. Like many freshwater fishes (Collette et al. 1977), the percids are considered to have a riverine ancestry.

Large moderate-to-low gradient rivers have oxbows, sloughs and embayment habitats that are

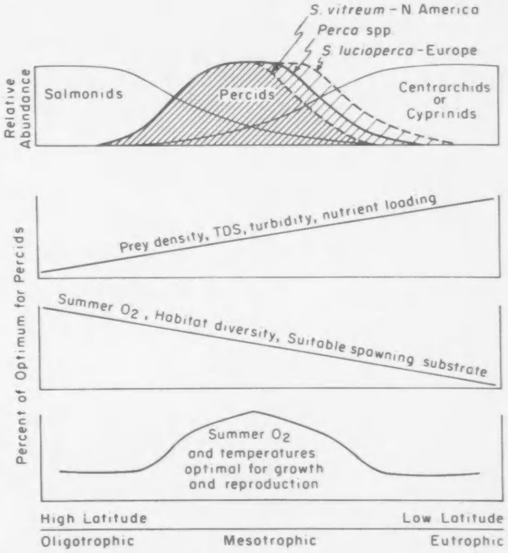
S. vitreum – N. America
Perca spp.
S. lucioperca – Europe
Relative Abundance
Salmonids
Percids
Centrarchids or Cyprinids
Percent of Optimum for Percids
Prey density, TDS, turbidity, nutrient loading
Summer O2, Habitat diversity, Suitable spawning substrate
Summer O2 and temperatures optimal for growth and reproduction
High Latitude
Low Latitude
Oligotrophic
Mesotrophic
Eutrophic

FIG. 1. Relation of optimum conditions for the percid fishes *Perca* spp. and *Stizostedion* spp. to geographic gradients and trophic status of the ecosystem.

analogous to those of the lacustrine littoral zone inhabited by *Perca* spp. Pools provide habitats equivalent to that of the lacustrine sublittoral zone, i.e. low current velocities and low light levels suitable for *Stizostedion* spp. As in lakes, thermal stratification and oxygen depletion are minimal. Temperature conditions also vary seasonally, allowing gonad maturation, but do not exceed upper tolerance limits (Hokanson 1977). Diel light cycles allow *Stizostedion* spp. to forage throughout the equivalent of the lacustrine littoral. Suitable spawning substrate and conditions for development are satisfied as well in rivers as in the littoral and sublittoral of lakes. The analogy is graphically presented in Fig. 2.

Perca spp. inhabit both the littoral and sublittoral zones. *Stizostedion* spp. are limited to the sublittoral during periods of high light intensity and/or thermal stratification but are released to forage throughout both zones during the diel light cycle. All four species may make foraging forays through the thermocline. All four species may also make pelagic migrations during a diel period, but *Perca* spp. must return to the littoral or sublittoral substrate at night (Thorpe 1977); and typically, *Stizostedion* spp. rest on the substrate by day (Regier et al. 1969). As *Perca* spp. are major prey items of *Stizostedion* spp., distributions are often similar.

In rivers and in lakes that are not strongly stratified in midsummer, the habitat of the four species extends throughout. Large surface area has little constraint on distribution. The entirety of such large systems as Oneida Lake, Red Lake, western Lake Erie, and Lake Balaton may be suitable habitat. In thermally stratified lakes, the habitat may be bounded by the intersection of the thermocline and the substrate. Due to the substrate orientation of these fishes, both small and large deep lakes in this group have percid habitats in a band peripheral to the hypolimnion (Fig. 2). During summer stratification, the lower depth limit approximated by the thermocline is very sharp in small systems but less well defined in large lakes. In the largest of deep lakes (e.g. Huron, Michigan, Superior, and Ontario), where the littoral substrate of exposed shoreline may be unsuitable for spawning due to strong wave action, the stocks may be restricted to bays or the relative proximity of a major spawning area (Spangler at al. 1977). As in shallow systems, diel light cycles allow *Stizostedion* spp. to range into the littoral zone. At lower latitudes, high epilimnion temperatures and oxygen depletion in the hypolimnion during summer may force aggregation at the intersection of the metalimnion and lake bottom, causing a substantial restriction of habitat (Kitchell et al. 1977; Fitz and Holbrook unpublished data).

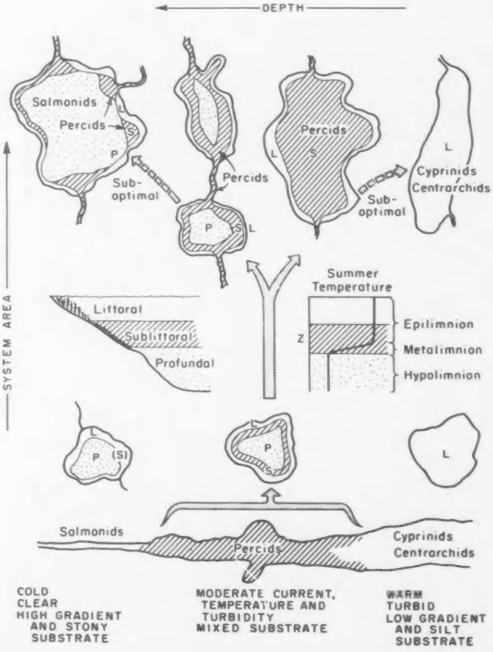

FIG. 2. Graphic representation of the river hypothesis. Optimum habitat for the percid fishes *Perca* spp. and *Stizostedion* spp. is defined by the littoral (L) and sublittoral (S) environmental equivalents to riverine conditions. Habitat boundaries are broadly defined in plan view as functions of lake depth (z) and surface area. Midsummer temperature profiles define the lower depth limit of the habitat as that of the lower boundary of the thermocline and upper limit of the profundal (P) zone. The upper boundary of the sublittoral corresponds to the compensation depth of light.

To restate, we propose that the habitats of *Perca* spp. and *Stizostedion* spp. in lakes are the equivalent of riverine extensions into the lacustrine environment. Where the area of habitat equivalence is large, as in shallow lakes, so are percid populations (e.g. Lake St. Clair, Lake Oneida, Red Lake, Saginaw Bay, western Lake Erie). Where the area is small in relation to total lake area, as in large, deep lakes, percids represent a lesser component of the total system (e.g. other Laurentian Great Lakes and many large, deep Canadian Shield lakes). Similar analogues exist for the European percid counterparts (e.g. Lake Balaton, the Caspian Sea, Lake Windermere, Dutch lakes), given that the European species are more tolerant of eutrophic conditions and higher temperatures (Marshall 1977; Thorpe 1977).

Independent evidence supports our hypothesis. The evolutionary origins and spread of the percids appear to have been within a fluvial environment (Collette et al. 1977). Reproductive patterns of percid species reflect adaptation to the fluvial environment (Balon et al. 1977). In Australia the introduced species, *P. fluviatilis*, spread through river systems and established a largely fluvial life-history pattern (Weatherly 1977). *Stizostedion lucioperca* dispersed and increased rapidly after being introduced to the river systems of the United Kingdom (Wheeler 1974). At the southerly limit of its range in North America, *S. vitreum vitreum* is generally confined to rivers or thermally stratified systems where the habitat is restricted by high summer temperatures (Collette et al. 1977; Fitz and Holbrook unpublished data). We suggest that restriction to rivers at the southerly distributional limit represents the ancestral habitat, i.e. that to which the organism is best adapted.

The distributions of many invertebrate species also suggest similar habitat conditions in rivers and the littoral plus sublittoral of lakes. Wesenburg-Lund (1908) and Ekman (1915) observed that the fauna of the nearshore zone of large European lakes contains many species usually thought to be typical of rivers. In North America Rawson (1930) found a variety of stream insects in the nearshore zone of Lake Simcoe, including the stonefly *Perla* sp., mayflies of the genera *Baetis*, *Choroterpes*, *Centroptilum*, and *Baetisca*, and the caddisflies *Hydropsyche* and *Helicopsyche* spp. He stated that the active washing of waves on stony shores provided "a substitute for the running streams" which are the usual habitat of these forms. Similar observations were made by Langlois (1954) for western Lake Erie and by Barton (1976) for the St. Lawrence Great Lakes.

Conclusion

An immediate question arises: Why aren't *Perca* spp. and *Stizostedion* spp. abundant in rivers today? They are, in fact, common in large, relatively unperturbed river systems. Regier et al. (1969) noted that "the walleye, throughout its range, is a fish of larger streams and rivers and certain types of lakes." Few of today's major rivers have not been altered by human activities. In many cases, large mesotrophic rivers have become highly eutrophic. The more eutrophication-tolerant European species have maintained well-developed river populations. The North American species, being less tolerant, have reduced abundance in the many river systems currently subject to cultural eutrophication. They have, however, become abundant in the river-habitat equivalents found in the littoral and sublittoral of many recently glaciated lakes.

We emphasize that most lakes in North America and Europe are of recent origin. Thousands of lakes currently inhabited by percid species have been invaded only since the last glaciation. Cultural eutrophication of many postglacial oligotrophic ecosystems has, in fact, increased their suitability for percids (Fig. 1).

We do not propose that all environmental conditions in large rivers are met in the lacustrine equivalent. We do suggest that environmental conditions important to *Perca* spp. and *Stizostedion* spp. may be found in lacustrine and river systems. As perceived, the habitat is not strictly proportional to lake area except in shallow systems.

The river analogies we ascribe to percid habitats in lakes may be similarly applied to the habitat requirements of certain salmonids (e.g., *Salmo* spp.), centrarchids (e.g., *Micropterus dolomieu*), and cyprinids (e.g., *Cyprinus* spp.) (Fig. 2). Salmonids dominate percids in systems of low productivity and low mean temperature, conditions more typical of high-latitude rivers and headwater streams. Centrarchids in North America and cyprinids in European waters dominate percids in more productive, warmwater environments, conditions represented in low-latitude streams and the lower reaches of many major rivers. With appropriate modifications to the variables specified in Table 1, the same generalizations apply in linking riverine conditions to those existing in the littoral and sublittoral of lakes.

The areal correlate is largely that of the littoral and sublittoral zones in large deep lakes. Small lakes connected by rivers represent a single, contiguous habitat rather than isolated basins. Spawning requirements constitute the Achilles heel of populations in large lakes. Human influence may be greatest when spawning aggregations occur in rivers or in the littoral environment. Most importantly, we suggest that the conceptual model (Fig. 2) provides a direct appraisal of habitat within lakes and drainage basins. The river analogy thus allows a more incisive perspective for management and research.

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Species Interactions in Percid Communities[1]

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MACLEAN, J., AND J. J. MAGNUSON. 1977. Species interactions in percid communities. J. Fish. Res. Board Can. 34: 1941–1951.

Evidence for species interactions in communities with *Perca* and *Stizostedion* is evaluated. Substantial evidence exists for the importance of predation by and on percids to community structure and function. Some evidence also clearly demonstrates that competition is an important interaction both within *Perca* populations and between *Perca* and other species. The necessity of using manipulative experiments to test for community level effects of competition and predation is emphasized. Such manipulative experiments, however, should be restricted in number and conducted with great care, because the community changes they induce are often irreversible and detrimental.

Species interactions related to feeding have apparently resulted in the partitioning of habitat and food resources among fishes in percid communities. Partitioning of space is considered in terms of distribution of *Perca* and *Stizostedion* in respect to temperature in stratified and unstratified aquatic systems. In stratified lakes, percids are expected to be spatially segregated from fishes with other thermal requirements, such as the warmwater centrarchids and the cold-water salmonids. Seasons and depths of potentially intense interactions are diagrammed. In unstratified lakes, latitude and lake size set the stage for the thermal habitat that favors the physiology of percids in some systems. Resource partitioning, in respect to food size and time of day for foraging, is also diagrammed and appears to be important. It is argued that species interactions between other fishes and *Perca* and *Stizostedion* are greatly reduced by present patterns of resource utilization.

Key words: competition, predation, resource partitioning, percid communities

MACLEAN, J., AND J. J. MAGNUSON. 1977. Species interactions in percid communities. J. Fish. Res. Board Can. 34: 1941–1951.

Nous examinons les preuves d'interactions des espèces dans les communautés avec *Perca* et *Stizostedion*. On a de bonnes preuves de l'importance de la prédation par et sur les percidés par rapport à la structure et la fonction de la communauté. Certains signes démontrent également que la concurrence est une interaction importante à la fois au sein des populations de *Perca* et entre *Perca* et les autres espèces. Nous faisons ressortir la nécessité de faire appel à des expériences de manipulation pour vérifier les effets, au niveau de la communauté, de la concurrence et de la prédation. De telles expériences, cependant, doivent être rares et effectuées avec beaucoup de précaution, car les changements qu'elles déclenchent dans la communauté sont souvent irréversibles et dommageables.

La partition de l'habitat et des ressources alimentaires parmi les poissons présents dans les communautés de percidés a, semble-t-il, déclenché des interactions entre espèces en relation avec l'alimentation. Nous examinons la partition de l'espace en fonction de la répartition de *Perca* et de *Stizostedion* avec la température dans des systèmes aquatiques stratifiés et non stratifiés. Dans les lacs stratifiés, on s'attend que les percidés seront séparés dans l'espace des

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poissons dont les exigences thermiques sont différentes, tels les centrarchidés d'eau chaude et les salmonidés d'eau froide. Nous représentons schématiquement les saisons et les profondeurs d'interactions intenses possibles. Dans les lacs non stratifiés, la latitude et la grandeur du lac créent un milieu thermique qui favorise la physiologie des percidés dans certains réseaux. Nous présentons de façon schématique également la partition des ressources, apparemment importante, selon la grosseur de la nourriture et l'heure à laquelle les poissons se nourrissent. Nous soutenons que les modalités actuelles d'utilisation des ressources réduisent considérablement les interactions entre les autres espèces de poissons et *Perca* et *Stizostedion*.

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THE intensity and pattern of competition and predation are central to hypotheses that attempt to explain the structure and function of biological communities (Addicott 1974). Feeding interactions are a primary means by which one species influences the population of another. These species interactions include predation, competition, and parasitism.

Species interactions are discussed in numerous papers of this symposium as either causes for or indicators of stress in fish communities. In this paper, we consider predation and competition in communities with *Perca* or *Stizostedion*. These communities are referred to as percid communities. An introduction to the ecology of fish parasites can be found in Dogiel (1961) and in Kennedy (1975, 1977).

We are interested in three questions about species interactions:

1) Do interactions occur between percids and other species? This is a trivial question in relation to predation, but competition between species is difficult to demonstrate. We discuss the problem of what evidence is required to show that competition occurs.

2) How strong are interactions between percids and other species? MacArthur (1972) reasoned intuitively that interactions are neither so weak that other species invade the system nor so strong that populations are unstable. The problem of quantifying intensity of interactions is briefly discussed.

3) What are the results of species interactions in percid communities? Species appear to coexist in communities by partitioning of food, space, and time. We assume that patterns of resource utilization and partitioning result from coevolution driven by competition and predation as selective mechanisms rather than by chance occurrence of species with different resource utilizations. We diagram a simplified view of resource partitioning by percids in space, food, and time, that apparently evolved from species interactions in the dim and distant past. A problem with this approach is that we cannot necessarily determine the selective mechanisms that resulted in the observed patterns of resource utilization from an examination of the present state of the system (Vandemeer 1972).

Predation in Percid Communities

Predation is intense by percids and on percids, and both processes have significantly influenced the structure of percid communities (Popova and Sytina 1977; Holčik 1977; Lind 1977; Bonar 1977). *Stizostedion* as a predator seems to have a larger effect on the community than other predators such as northern pike, *Esox lucius*. *Perca* have a large influence on their own population structure because of cannibalism, both in monospecific (see Popova and Sytina 1977) and in more complex communities (Holčik 1977).

The evidence required to demonstrate predation is straightforward, as either stomach analysis or direct observations will usually suffice. But evidence required to measure predation intensity (Popova and Sytina 1977) or population consequences of predation (Holčik 1977) is not simple or straightforward. We often depend on correlative data from natural communities. The discussion that follows on competition points out research approaches that are just as pertinent for predation as for competition, but with the same problem — that the influences of predation and competition often cannot be separated.

Competition in Percid Communities

Two or more organisms will compete when they seek a common limiting resource which occurs in insufficient supply to meet their combined requirements (Birch 1957). While we may not agree on a precise definition, the criteria required to demonstrate competition between two species have been defined by Reynoldson and Bellamy (1972). These are that (1) the comparative distribution and/or relative abundance of potential competitors should be consistent with the hypothesis that competition occurs, (2) the species use a common resource for which competition can occur, and (3) evidence on fecundity, survival, growth, or some other appropriate factor indicates that intraspecific competition also occurs. In addition, (4) both the resource and the population should be manipulated, with appropriate controls, and results should be consistent with the competition hypothesis. As Reynoldson and Bellamy (1972) pointed out, manipulation of absolute amounts of the resource is not necessarily sufficient because resource availability also may vary independently of the competition intensity. Finally, (5) events following the manipulation, i.e. introduction, removal, or reduction of one species, should be consistent with the competition hypothesis.

These criteria involve indirect (the first three) and direct (the last two) evidence for competition. Indirect evidence, such as correlations between population sizes, displacements, replacements, character divergence, and niche differences, is necessary, but only manipulation experiments provide a critical test. Even then, the system must be well enough known to exclude or at least evaluate direct effects of predation as a factor.

Manipulative experiments — We have some evidence for competition between a percid and other species. Good examples are scarce because, even though species have frequently been introduced or removed from systems, usually the manipulations were not followed quantitatively or with adequate controls. Below we discuss experiments to test hypotheses about interspecific and intraspecific competition in percid communities.

Johnson and Hale (1977) gave evidence to support the hypothesis that competition occurs between white suckers, *Catostomus commersoni*, and yellow perch, *Perca flavescens*, in Wilson Lake, Minnesota. The abundance, growth rate, and condition factor of perch increased after removal of 85% of the biomass of adult suckers. Later, when perch increased in abundance, their growth rate and condition declined. Before sucker removal, yellow perch, common sucker, and walleye, *Stizostedion vitreum vitreum*, shared several food organisms, particularly immature burrowing mayflies. After sucker removal, large yellow perch shifted their diet from small crustaceans to larger immature insects, particularly mayflies, and young perch ate more crustaceans.

The responses of walleye to sucker removal were not as clear, perhaps because they were due in part to changes in the perch population. Growth rates of adult walleye increased for 6 yr after removal and declined later as their abundance increased. Exceptionally large year-classes of walleye were produced. Young walleye ate more small crustaceans, dipteran larvae, minnows, and darters than before sucker removal, while the percentage of minnows and darters in the diet of larger walleyes decreased as young perch and mayflies increased in importance.

A difficulty in the interpretation of these results is the absence of controls and replicates. There was only one manipulation in one lake. However, the data strongly support the hypothesis that competition occurred between common suckers and yellow perch in the lake. Food seemed to be the limiting resource, as judged from changes in food habits, growth rate, and condition, but competition between common suckers and walleyes for spawning sites (Schupp and Macins 1977) may also have been involved.

A second manipulation experiment supports the hypothesis that competition occurs between yellow perch and three salmonids: brook trout (*Salvelinus fontinalis*), rainbow trout (*Salmo gairdneri*), and splake (*Salvelinus namaycush* × *S. fontinalis*) (Fraser unpublished data). Combinations of two of the three salmonids were stocked each year in Little Minnow Lake in Algonquin Park, Ontario, during 1962–73. Yellow perch were first observed in 1967, and mark-and-recapture estimates showed that a large population was quickly established. A rapid decline in their growth rates suggests that intraspecific competition occurred. Production and growth rates of all three salmonids declined. Initially, diets of yellow perch and salmonids overlapped considerably, but as perch increased in abundance, two species (brook trout and splake) shifted their food habits to smaller items. Results are consistent with the hypothesis that competition occurred between yellow perch and the three salmonids.

Manipulation experiments have also been conducted to test the hypothesis that intraspecific competition occurs in perch populations. Growth rates of *Perca* spp. are extremely variable (Thorpe 1977), and reduced growth rate, or "stunting," is usually considered a phenotypic response to intraspecific competition (Alm 1946, 1952). Growth of perch in stunted and unstunted populations is similar for the first 2 yr, but in stunted populations it declines rapidly in subsequent years (Alm 1952; Deelder 1951).

A natural reduction in population size of *Perca fluviatilis* in a Swedish lake was correlated with increased growth rate (Alm 1946). The removal of large numbers of perch in Lake Windermere was followed by an initial increase in growth rate (LeCren 1958), but growth continued to increase after changes in population size had ceased, so

TABLE 1. General evidence for resource partitioning in temperate freshwater fishes in North America and Europe on the basis of thermal requirements and dominant food type. (Compiled from the collective views of the working group. Definition of thermal classification in Hokanson 1977.)

Thermal classification	North America			Europe		
	Zooplankton	Benthos	Fish	Zooplankton	Benthos	Fish
Temperate-zone eurytherms	*Lepomis* *Pomoxis* *Notropis* *Clupeus*	*Micropterus* *Lepomis* *Ambloplites* *Ictalurus* *Aplodinotus* *Gasterosteus* *Pungitius*	*Micropterus* *Lepisosteus* *Amia*	*Albernus* *Pelecus* *Scardinius*	*Rutilus* *Pungitius* *Gasterosteus* *Cyprinus* *Blicca* *Tinca*	*Aspius* *Silurus*
Temperate-zone mesotherms	*Perca*	*Perca* *Etheostoma* *Catostomus* *Percina* *Percopsis*	*Perca* *Stizostedion* *Esox*	*Perca*	*Perca* *Gymnocephalus* *Abramis*	*Perca* *Gymnocephalus* *Stizostedion* *Esox*
Temperate-zone stenotherms	*Coregonus* *Osmerus*	*Coregonus* *Cottus* *Lota* *Myoxocephalus* *Etheostoma* *Salvelinus*	*Lota* *Salvelinus* *Salmo*	*Coregonus* *Osmerus*	*Coregonus* *Cottus* *Myoxocephalus*	*Lota* *Salmo*

that growth rate and population size were not correlated. LeCren suggested that the reduction had a direct effect initially on growth rates of remaining adults, but that the continued increase in growth rate was due to a gradual increase in abundance of benthos. Reductions in numbers of yellow perch in North American lakes have generally led to increased growth of adults (Rutledge and Barron 1972).

Experiments to determine the relative importance of food quantity and particle size, or even space, as critical resources for perch are wanting. Rapid growth of perch in Swedish and Dutch lakes appears to be related to availability of forage fish. Introduction of *Gambusia* sp. into ponds with stunted perch populations provided a forage fish, and perch growth increased rapidly (Thorpe 1977). Abundant small perch were important determinants in development of a group of fast-growing piscivorous or cannibalistic perch (Holčik 1977; Popova and Sytina 1977). The presence of suitable size prey is apparently an important feature for fast growth by perch.

In summary, the evidence supports the hypothesis that intraspecific competition occurs within perch populations, the limiting resource apparently being suitable kinds of food.

The manipulation experiments above are simple, but more complete experiments to clarify mechanisms of interactions within and between species should be possible, at least in systems with only a few species. To be useful, such experiments should be designed to test a hypothesis complex enough to represent the essentials of the ecosystem. To be able to say that competition exists or not is insufficient. Development of simulation models of such systems is probably a necessary step if we are to know whether an experiment verifies anything of substance.

Unfortunately, manipulative experiments in natural ecosystems have the potential to irreversibly alter or degrade the community. Consequently, the impact of such experiments must be evaluated before an experiment is proposed, especially if the manipulation is the introduction of a species new to the lake (Magnuson 1976; Magnuson et al. 1975). Consideration should be given to whether the experiment is reversible, whether the organism will escape into adjacent lakes and watersheds, whether the animal will have effects on the community other than those desired, and whether the expected changes will negatively influence present users of the lake.

Intensity of Competition

The estimate of intensity of interspecific competition should, in some sense, be the ratio of the difference between a species performance alone and its performance in the presence of the competitor species divided by the difference between the species performance alone and its performance in the presence of itself (Vandemeer 1972). The latter term (the effect of a species on itself) would be an estimate of intraspecific competition. A central problem in attempts to quantify effects of interactions and the niche is the choice of an appropriate index of performance. Growth was used as a performance index in manipulation experiments above. This assumed a correlation between growth and fitness components, such as fecundity. Kerr (1977) proposed Fry's scope for activity as a performance–fitness measure to quantify niche parameters. Slobodkin and Rapoport (1975) suggested that organisms respond to environmental change with a hierarchical set of adaptations that range from rapid response at the behavioral and physiological level to slower responses at the level of population and gene pool. We must decide at which level we will choose our measures of performance.

Two fundamentally different approaches can be used to estimate intensity of competition (Vandemeer 1972). The first is an experimental approach, based on manipulation experiments with appropriate controls, to estimate performance. A simple example would be experiments like Fraser's (unpublished data) on salmonids and yellow perch, to obtain estimates of growth alone, with itself, and with other species. A second is an observational approach that assumes an equilibrium state for populations. Performance measures are averaged over a large enough set of lakes so that effects of factors other than those involved in the interaction process are eliminated. For example, growth of yellow perch in lakes with and without common suckers might be compared.

Several problems exist in the use of experimental manipulations and observations to measure competition coefficients in fish communities. Relations between two species are complicated by age- and size-related changes in resource utilization. Also, we are not able to separate competition and predation components of the general interaction coefficient. If, for example, common suckers eat yellow perch eggs, we cannot determine whether the removal of suckers caused an increase in numbers of perch because competition was reduced or because egg predation was reduced. Nonlinearities and multiple stable points for species composition mean that estimates of interaction coefficients based on manipulation experiments are influenced by the particular assemblage of species (Neill 1974). Interaction coefficients from manipulative experiments must be considered approximations, because intensities of interspecific competition and other interactions continually shift with the continual flux in physical and biological habitats (Johannes and Larkin 1961; Zaret and Paine 1973).

Competition is central in current hypotheses concerning structure and function of communities. Manipulation experiments, with particular attention paid to measurement of responses and model testing, should be a fruitful approach to increase our knowledge at the community level.

Resource Partitioning

Species interactions related to feeding apparently have resulted in the partitioning of habitat and food resources among fishes in percid communities. Effects of competition and predation cannot be separated in these observations and speculations about resource partitioning. If a difference in response to temperature is observed among species, we cannot determine whether it resulted from competition or from interactions between the predators and their food. The predation process itself may be instrumental in the evolution of resource partitioning. One way of viewing predation is through the eyes of "optimum foraging theory" (G. H. Pyke, University of Utah, Salt Lake City, personal communication). This theory is based on the idea that predators maximize the ratio between the quantity (usually energy) eaten and time or energy they expend to obtain the food. The process usually involves selection of a prey with the most energy per time spent eating by the predator, selection of optimum habitat in which to forage, allocation of foraging time to habitat patches, and optimization of food search.

Examples below of resource partitioning involve temperature, food particle size, and time of day, as dimensions of the niches of *Perca* and *Stizostedion*. Even though these three niche parameters are important, we do not wish to imply that other factors are not important in the complete description of an "N" dimensional niche for a percid. Other niche dimensions, such as light intensity (Ryder 1977) and spawning requirements (Balon et. al. 1977), are omitted here only to simplify examples.

Even at a very crude level of resolution, evidence demonstrates that resource partitioning in percid communities does occur (Table 1). *Perca*, *Stizostedion*, *Gymnocephalus*, and some etheostomids are temperate-zone mesotherms as defined by Hokanson (p. 1524, 1977). It is important to review these definitions before going farther. Temperature optima and preferred temperatures of these species segregate them during summer from temperate-zone eurytherms such as centrarchids and temperate-zone stenotherms such as salmonids (Hokanson 1977; Kitchell et al. 1977). Similarly, major differences in food type further reduce the potential for com-

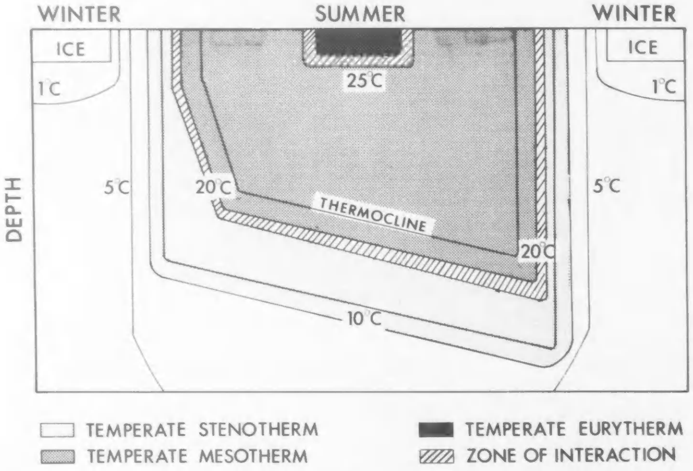

FIG. 1. Seasonal changes in preferred thermal regions of fishes in a stratified temperate lake with indications of spatial and temporal overlaps among major thermal groups. Thermal classification of fishes is taken from Hokanson (1977).

petition among these more common species. At this level of classification *Perca* adults appear to be habitat specialists in regard to temperature, but food generalists in that, depending on the condition of the lake, they eat zooplankton, benthos, or fishes (see Popova and Sytina 1977). Also, *Stizostedion* adults appear to be food specialists, eating primarily fishes, at this level of food habit classification, as well as thermal habitat specialists.

Temperature — Habitat segregation of percids from centrarchids and salmonids on the basis of temperature is most nearly complete when temperate-zone lakes are thermally stratified in summer (Fig. 1). By midsummer, deep lakes and those with a small fetch have a broad range of temperature containing not only those preferred by temperate-zone mesotherms such as *Perca* but also those preferred by temperate-zone eurytherms like centrarchids and temperate-zone stenotherms like salmonids. Often the warm temperatures preferred by centrarchids are available only in the littoral zone, which potentially even further spatially segregates the centrarchids from the percids. *Perca* and *Stizostedion* are then spatially segregated from potential interactions with centrarchids and salmonids by distributional responses to temperature (Ferguson 1958; Neill and Magnuson 1974; and Engel and Magnuson 1976). At this season, metabolic processes and demands by consumers for food resources in the lake are maximum.

In stratified temperate-zone lakes a potential for intense interaction between percids and salmonids occurs in early spring and late fall and between percids and centrarchids in late spring and late summer (Fig. 1). During these seasons, percids cannot use temperature to spatially segregate from species that prefer warmer or cooler water, because the preferred temperatures are not available for each group. Consequently, for a time they must share habitats that have the same temperature. Interaction may be intense because temperatures, and consequently, rates of feeding and metabolism, are moderately high. When these interactions occur, percids should have the advantage over the centrarchids, since centrarchids are not at their most preferred temperatures, and salmonids should have the advantage over percids and centrarchids, because in early spring and late fall available temperatures are optimum only for salmonids. See Kitchell et al. (1977b) for simulation of seasonal growth of percids, centrarchids, and salmonids.

During winter (Fig. 1) these species are not expected to segregate by temperature, since all would be expected to, and apparently do (Engel and Magnuson 1976; Magnuson and Karlin 1970), prefer the warmest water available (ca. 4°C). However, potential interactions are probably reduced in intensity because metabolic processes and food demands are low.

Interactions among percids are expected to be most intense from late spring to late fall, when they are most segregated from temperate eury-

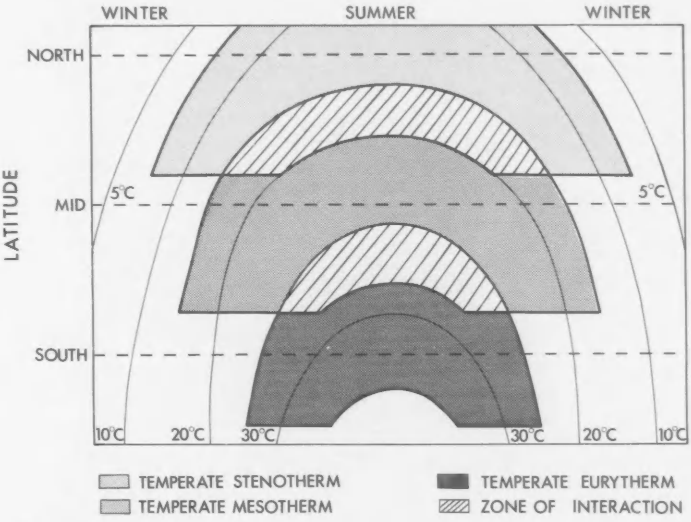

FIG. 2. Seasonal changes in optimum thermal regions of fishes in unstratified lakes in relation to latitude with indications of spatial and temporal overlaps among major thermal groups. Thermal classification of fishes is taken from Hokanson (1977).

therms and temperate stenotherms and are themselves concentrated in strata of the lake with their preferred temperature (Fig. 1).

Thermal segregation of fishes in a stream ecosystem can be considered in analogy with the stratified lake. In summer the headwaters tend to remain cool, while the lower reaches warm to a greater extent. In spring and fall, temperatures are more nearly uniform along the entire stream from headwaters to the mouth, analogous to spring and fall overturns in lakes. Perhaps temperate-zone mesotherms, eurytherms, and stenotherms redistribute along the river on a seasonal basis with greater isolation during summer.

The role of temperature on potential species interactions is somewhat different both for lakes that do not thermally stratify or have anoxic deep water in summer and for rivers considered at a single location (Fig. 2). In these cases there is little opportunity to segregate on the basis of temperature because the temperature range available at any one time is narrow. However, summer temperatures depend in part on the latitude and size of the lake and favor groups of fishes with temperature optima closest to the summer temperatures (Kitchell et al. 1977a). Physiological rather than distributional responses to temperature are most important here, in contrast to stratified systems. Potential interactions among percids are expected to be most intense when summer temperatures are near their optima such as at midlatitudes (Fig. 2). At slightly warmer summer temperatures to the south, interactions of percids with temperate-zone eurytherms should intensify. At slightly cooler temperatures to the north, interactions with temperate-zone stenotherms should intensify. Seasonal changes in the intensity of interactions should vary with latitude, the interaction with centrarchids being most intense in midsummer and that with salmonids in spring and fall. The assumption is that predation and competition are most intense when the temperature is within the optimal range of two groups.

The diagrams (Fig. 1, 2) are greatly stylized and simplified, and the inferences on intensity of interactions are hypotheses, not fact. Also, actual temperature preferences and temperature optima differ within these thermal groups of fishes (Hokanson 1977) such that separation among groups is not as distinct as in the diagrams. Many fish species have a preferred temperature range about 4 deg C wide (Neill and Magnuson 1974), but widths of physiological optima are broader. In addition, the distributions of their prey, predators, and competitors influence the actual temperatures occupied in a given situation (Magnuson and Beitinger 1977). Such plasticity in response to species interaction is probably the most common means by which species modify their niches to adapt to environmental change. Such changes

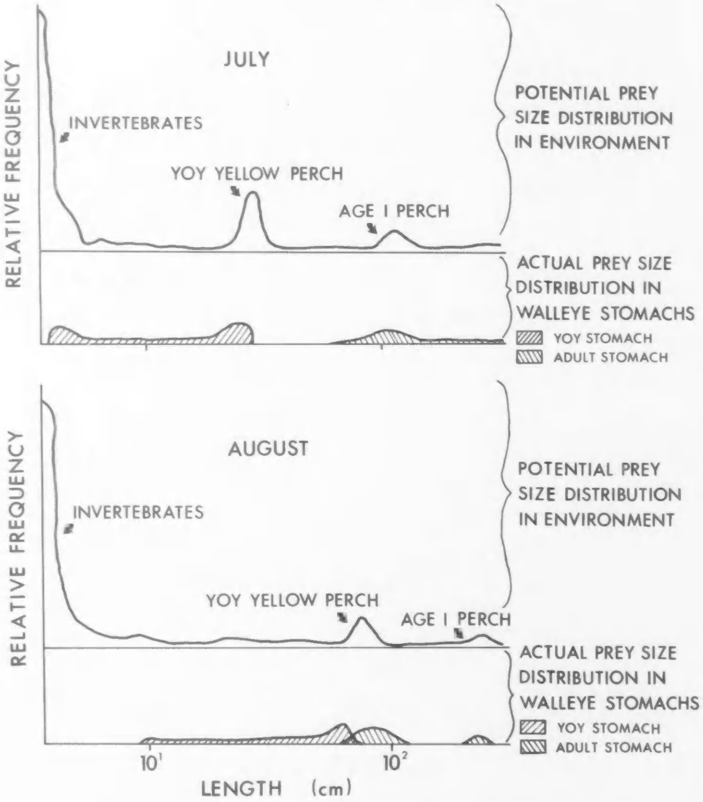

FIG. 3. Potential and actual prey size distributions of walleye in July and August as developed by Forney during the PERCIS Symposium on basis of Oneida Lake, New York.

in reference to food habits are referred to as niche shifts (Werner and Hall 1976), or interactive segregation (Nilsson 1967).

Prey size — The size spectrum of prey available to *Perca* and *Stizostedion* ranges from zooplankton to fish. Pulses of zooplankton, emergence of insects, and recruitment of young fish during a season present the percids with a continuously changing array of particle sizes. Although percids are capable of utilizing a broad size range of prey (Popova and Sytina 1977), discontinuities in the size distribution are often critical in the 1st yr of life (Fig. 3). The earliest stages would be most critical because young percids eat relatively large prey and only a narrow range of sizes (Popova and Sytina 1977).

Shifts of diet to larger forms is common among percids as they grow (Popova and Sytina 1977; Spanovskaya and Grygorash 1977). In North America (Forney 1966) walleye often shift from a diet of zooplankton to yellow perch when perch are 15–25 mm long. If yellow perch are either scarce or too large, walleye continue to utilize invertebrates and growth is retarded. Often only the larger walleye in a year-class are capable of feeding on perch, and smaller walleye are restricted to a diet of invertebrates (Fig. 3). By fal! the length distribution of young walleye is skewed or bimodal with planktivorous and piscivorous members of the year-class clearly separated

Production of young-of-the-year perch may largely determine the forage for walleye in lakes where fish diversity and thus alternative prey density is low. Growth rate of young walleye must closely match the growth of its prey (Morsell 1970). Larger percids have greater food size flexibility. Yearling and older walleye frequently feed on age 1 perch or cisco, *Coregonus artedii*, in early summer, shifting to the young-of-the-year in late summer (Fig. 3). In simple systems where young perch are the primary prey, the failure of a perch year-class increases walleye predation on other species and produces synchronous fluctuations in year-class sizes of associated prey species (Forney 1974). Such effects of species interaction could easily and mistakenly be interpreted as the influence of a density-independent (abiotic) factor.

Percids in North America have apparently evolved in a relatively simple predator–prey complex which results in large gaps in the prey size continuum (Fig. 3). Low prey diversity may explain the sensitivity of many northern lakes to introduction of walleye. Added prey exploitation must induce instability and the process of restructuring the prey community may be prolonged, as observed in Escanaba Lake (Kempinger and Carline 1977). *Perca* and *Stizosterion* also significantly modify the structure of fish communities in European and Asian lakes (Popova and Sytina 1977; Holčik 1977; Lind 1977).

Research on optimum foraging by *Perca* and *Stizostedion* during development to explain shifts from one prey to another would be especially useful.

Time

Partitioning the time of feeding or use of habitat is also suggested in the data on juvenile and adult percids (Fig. 4). The timing of feeding throughout the diel period is especially important in the availability of prey to *Perca* and *Stizostedion* (Manteufel et al. 1965). Both genera tend to feed most intensely at dawn and dusk, but *Perca* generally continue feeding during the day, while *Stizostedion* feed more at night. Dawn and dusk periods are particularly important; prey are then most vulnerable to *Stizostedion* because the latter see well at low light intensities (see Ali and Anctil 1977; Ali et al. 1977; Ryder 1977), and because the prey alter their distribution and behavior when light intensity is changing. After their larval stages, *Perca* school off the bottom inshore or offshore during the day (Engel and Magnuson 1976), but at dusk the schools disperse and the fish move inshore. Adults settle to the bottom (Hasler and Villemonte 1953), but post-larval young-of-the-year seem to move toward the surface (Kelso and Ward 1977). The dispersal of schools and poor low-light vision of *Perca* contribute to their vulnerability. Schools of small cyprinids also break up at this time, and they are also more readily available, not only to *Stizostedion*, but also to larger *Perca* (Manteufel et al. 1965). One interpretation is that the more diurnal habit of *Perca* has reduced either their interaction with or vulnerability to *Stizostedion* and that the nocturnal habit of *Stizostedion* increases for them the availability of large prey that are more photoptic. The dawn and dusk periods are a time of incomplete time partitioning in which interactions are most intense.

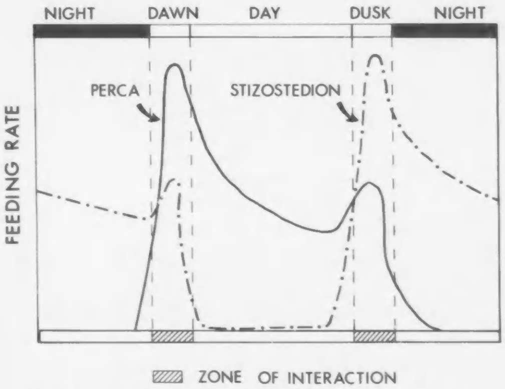

FIG. 4. Diel changes in feeding activity of *Stizostedion* and *Perca* indicating crepuscular pattern for intense interaction between these genera as developed by Popova during the PERCIS Symposium.

Conclusion

Predation, competition, and other species interactions apparently have resulted in resource partitioning in fish communities. *Perca* and *Stizostedion* are temperate-zone mesotherms and as a group have fewer species than temperate-zone stenotherms and temperate-zone eurytherms. Their particular cool-water niche segregates them in space from many other species and results in reduced species interactions. Species interactions that have marked influence on community structure and seem especially intense are predation by *Stizostedion* and cannibalism by *Perca*.

Predation as a species interaction is easier to demonstrate than competition because its definition does not include the significance of the population consequences of predation on the prey and predator populations. To demonstrate competition or the effects of predation, manipulative experiments in natural systems are needed. Even then, it is difficult to separate the independent effects of competition and predation. Thus, manipulative experiments require careful design, replication, and accessory observations to determine the influential processes.

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Niche Theory and Percid Community Structure[1,2]

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KERR, S. R., AND R. A. RYDER. 1977. Niche theory and percid community structure. J. Fish. Res. Board Can. 34: 1952–1958.

The Hutchinsonian definition of niche is conceptually attractive, but lacks a quantitative, operational basis for analysis. Fry's autecological theories remedy the deficiency by permitting the use of metabolic units of measure that are observable, common, and important to all organisms and ecological functional groups. Contouring the niche hyperspace in units of metabolic scope for activity enables analyses at both the autecological and synecological levels of organization. A simple analysis of four coexisting percid species illustrates some applications of the method.

Key words: community ecology, theory, Percidae, niche theory, prey size, light intensity, limiting factors

KERR, S. R., AND R. A. RYDER. 1977. Niche theory and percid community structure. J. Fish. Res. Board Can. 34: 1952–1958.

La définition de Hutchinson de la niche est conceptuellement attrayante, mais manque de fondement quantitatif et opérationnel pour en faire l'analyse. Les théories autécologiques de Fry remédient à cette déficience en permettant l'utilisation d'unités métaboliques de mesures observables, communes et importantes pour tous les organismes et groupes fonctionnels écologiques. Le fait d'établir les contours de l'hyperespace en unités de portée métabolique d'activités permet des analyses aux niveaux à la fois autécologiques et synécologiques d'organisation. Nous illustrons certaines applications de la méthode par une simple analyse de quatre espèces de percidés cohabitant.

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THE concept of niche has undergone considerable evolution since its introduction to the ecological literature by Grinnell (1917). In some sense, the term has been used by most ecologists. Most often, it has been seen as a characteristic of the organism, as if it were something the organism carries around with itself; but sometimes the niche has instead been viewed as an environmental characteristic, as exemplified by the term "vacant niche." Thus niche has been variously used to refer to an organism's diet spectrum, to its habitat, or, more often, to its environmental interactions in some broader sense (Geisel 1955; Udvardy 1959). We describe here a modification of a current niche definition, and illustrate its application as a quantitative analytical tool, useful at both the autecological and synecological levels of organization.

Theory of the Ecological Niche

Recently, at least for North American ecologists, the definition seems to have stabilized, in a form due to Hutchinson (1957, 1965). In brief, the Hutchinsonian niche consists in the abstract hypervolume that is generated by assigning a dimension to each factor that affects an organism's survival. The rapid and relatively general acceptance accorded such an admittedly abstract and nonoperational formulation suggests that it must in fact offer some measure of robustness and utility that may not be initially apparent.

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In our view, rapid acceptance of the current niche definition reflects the increased preoccupation of ecologists with process and function. Intuitively at least, Hutchinson's concept satisfies a need for a general method of describing an organism's functional status. In effect, the niche now serves as a convenient general descriptor at the interface between autecology and synecology. The essential aptness of Hutchinson's formulation is particularly clear in the light of the parallel and independent conceptual developments embodied in the work of Fry (Kerr and Lawrie 1976).

Working from the viewpoint of autecology, Fry has been concerned with quantitative ordering of the effects of the environment on animal activity. This aspect of his work, and that of his students and colleagues, has resulted in two major achievements (Fry 1947, 1971). First, it has resulted in precise, quantitative procedures for measuring the responses of organisms to environmental identities. In principle, the Fry paradigm provides rigorous, reproducible methods for delimiting and quantifying the otherwise ambiguous Hutchinsonian hyperspace. Second, Fry recognized the relation between an activity and its supporting metabolism, and provided a metabolically-oriented categorization of environmental factors which greatly simplifies the task of selecting the niche parameters that are appropriate to a given analysis. That is, Fry's classification of environmental factors provides a basic metabolic structure for organizing and treating the very large array of disparate factors which, taken together, determine the Hutchinsonian hyperspace. Specifically, we can contour the niche hyperspace in units of metabolic "scope for activity" (Fry 1947), providing measures of either the potential or the realized functional status of an organism, in units that are common to all components of a community (Kerr 1974).

A central concept of the Fry paradigm concerns his approach to the notion of "system," one which evidently antedates much of the current systems literature. In his terms, a "system" is "energy that is contained or channeled through a pattern of form," where "form is a pattern of forces" (Fry 1976, p. 333). Building upon this premise, Fry postulated the interaction of two basic sets of factors "the controlling factors, the state of activation of matter; and the limiting factors, which is the availability of matter." Thus the interplay of these two sets of factors, modified by the effects of supplementary factors in the Fry categorization, determine in concert the responses of organisms, as systems, to their environment (Fry 1976, p. 338). Clearly, Fry's autecological analysis provides a deep, incisive view of the boundaries and internal structure of the niche hyperspace.

We have summarized these views here, albeit briefly and incompletely, because in our opinion the powerful and complementary nature of Hutchinson's and Fry's work toward an integrated theory of the niche seems not to have been generally appreciated. It is our view that Hutchinson and Fry, working independently, have provided the basis for a cogent, integrated, and operational theory of the niche. Indeed, except for the extrapolation to *n*-dimensional phase space, the "zone of tolerance" explicated by Fry (1947) anticipates in many ways the current niche formulation, and does so in lucid, operational terms. In essence, we assert that Fry has provided the necessary concepts and procedures to implement the abstract, global model generated by Hutchinson. If we accept this much, it remains to determine the consequences and limitations of the Hutchinson/Fry niche.

Limitations of current theory — To begin with, it is essential to recognize that the hyperspace is necessarily *n*-dimensional, and that the niche definition is therefore open-ended. The alternative, formulation of a generalized niche structure that is bounded and finite, seems to us unachievable because of the inherent properties of ecological systems. We analyse systems by observing variables; there is no scientific alternative. But, clearly, any real entity offers an unlimited list of potential observables (Ashby 1956). It follows that a complete description of any real entity is inherently unbounded and operationally unachievable. The analyst, consequently, must work with the incomplete list of variables which comprises the system model. The analyst's system is therefore an incomplete representation of an open-ended "real" system (Kerr 1976).

The open structure of the niche is neither unique nor intractable. Indeed, MacArthur (1968) has noted the close similarity of niche with "phenotype," a concept which affords undoubted utility in a variety of applications. Incompleteness is an inherent aspect of the analysis of any real system and, if recognized, poses no insuperable difficulties. Unrecognized, it can and has caused confusion, as with the considerable obfuscation surrounding the trivial tautology of the "competitive exclusion principle." Niche analysis of any kind is therefore an approximation, based upon a selected list of variables that are judged to be relevant to the question at hand. As with any scientific analysis, it inevitably remains to determine in each instance whether the judgement is sufficient and "the analysis need be pushed no further" (Bronowski 1965).

A second fundamental consideration concerns the interactions among organisms. The effects of community interactions were included in the Hutchinsonian niche but are not directly amenable to the measurement techniques developed by the Fry school. For this reason, we suggest that parameterization of the Hutchinson/Fry niche be restricted somewhat, to exclude these interaction effects, which would themselves be measurable as indirect results in common units of net metabolic activity. That is, the niche thereby becomes a matrix within which the proportion of metabolic potential which is realized by the organism provides a measure of the otherwise intractable organism–organism interactions.

If this much be accepted, the way seems clear to apply the niche concept within the ecological context of a community analysis. The niche concept is fundamentally non-ecological unless such applications are feasible. Consider the generalized community depicted in Fig. 1, which arbitrarily comprises four species which we assume to be closely related ecologically, if not genetically, in the sense that an appreciable number of the 24 potential interaction pathways are functional.

There is a prevalent dictum among scientists that if all properties of the constituents of a system are known, together with full knowledge of the possible interactions among constituents, then full knowledge of the behaviors of the integral system can be generated (Ashby 1956). Although we are unconvinced of its validity for complex systems, we do not raise any particular quarrel with this view, because it suffices for present purposes to note that it is operationally irrelevant to ecological analysis (Kerr 1974). We have already discussed the fundamentally open nature of the niche specification for any organism, concluding that the analyst faces a basically subjective exercise of judgement in selecting the list of variables which seem sufficiently important to include in the system representation. We now raise the spectre that even if complete knowledge of the system components of Fig. 1 were available, the variety of potential interactions within even very small communities is very great, and approaching intractability even in the unlikely event that each possible interaction pathway is not in itself complex.

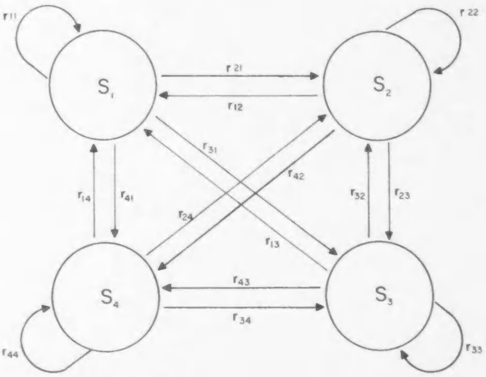

FIG. 1. Generalized interaction model. The S_i represent the state variables for species i, and the r_{ij} are rate coefficients for the effect of species i on species j.

A third fundamental consideration concerns incorporation of the time dimension in the Hutchinson/Fry niche. In the niche structure for an individual organism, time seems appropriately incorporated as a niche axis, although this in itself is not without its complexities. The Fry method of parameter evaluation admits of a time dimension, in the sense that the "zone of resistance" associated with each "zone of tolerance" incorporates units of time, and is precisely quantifiable. That is, for time units that are appreciably shorter than the generation time of an organism, proximate temporal effects can be incorporated with virtually any degree of resolution that is deemed sufficient. For longer time scales, however, the problem becomes highly complex, not simply because the generation times, hence appropriate time scales, of the various organisms of a community may differ appreciably but because the associated interaction effects are similarly dependent upon the various time scales. Thus each of the S_i of Fig. 1 represents more than a simple collection of state variables valid for a species during a given time interval; the S_i are also vectors in time. Thus we can incorporate, for example, such phenomena as growth effects and cannibalism within niche analyses at the community level.

Clearly, complete information will be unavailable to the analyst for any individual niche, and neither will the time-dependent interaction effects within a community be analytically tractable. It follows that the analyst must exercise judgement in selecting the list of variables which seem important, together with the major interaction pathways. Having done so, the analyst is faced with two options.

If the object of the analysis is to study integral properties of the intact system (persistence of a fish community, for example) then the integral behaviors must be observed directly as emergent properties before they can be associated with the underlying niche variables and interactions. A priori prediction of the integral behaviour of a system on the basis of incomplete knowledge of its structure is not possible (Kerr 1976), although such attempts are not infrequent in the ecological literature. In Fry's terms (Fry 1976, p. 333), "There is a way of coming back to autecology from synecology, but you cannot go the other way." Niche theory, within this constraint, provides a usefully generalized framework for analyzing community properties.

If the object of the analysis is to determine the status of the components of the community, then both qualitative and quantitative examination of the niche variables and interaction pathways provide useful analytical procedures. We briefly illustrate both aspects of niche analysis in the following section.

Niche Analysis of a Percid Community

With the foregoing theoretical framework in mind, we now consider some preliminary applications to percid ecology. In particular, we show that niche theory can provide a useful framework for such analysis, without necessarily becoming involved in elaborate analytical constructs, and without encountering vexing theoretical constraints.

Some further considerations from the ecological literature can usefully guide our analysis. Fry's fundamental premise that autecological systems are governed by two basic sets of factors, the controlling and the limiting factors, was noted earlier. In a useful sense, these basic sets are comparably applicable at the synecological level. There are factors which predominantly control the rates of ecological processes, in the sense that dynamic regulation prevails, and other factors which primarily limit processes, in the sense that variables are constrained without appreciable modification. In terms of Fig. 1, the controlling factors at the community level are those which primarily serve to modify the rate coefficients, r_{ij}, associated with the interaction pathways. The limiting factors are those which serve to select or constrain the conditions under which an interaction can occur at all.

From the voluminous theoretical literature which has treated simple interaction models, such as that of Fig. 1, we conclude that the continued survival of any component species requires, at the very least, something like a "refugium" (in a mathematical sense). That is, whether a model is binary, as with the most common applications of the ubiquitous Lotka–Volterra equation and its numerous variants, or some higher-order construct, as in Fig. 1, persistence of the system requires provision for something each species can "do," or "hide in," to the exclusion of its competitors. Smith (1972) has made this point clearly with his very general, three-cornered, "daisy chain" model. We conclude from evidence of this type that the persistence of a species in an interactive community presupposes the continuing existence of something that resembles a "refugium" in the most general sense of the word. This might be a spatial refuge, for example, or any other inhomogeneity which has similar mathematical effect on the equation system. It is factors of this kind that we regard for present purposes as limiting, in the sense that they exert a boundary constraint on the niche hyperspace.

The two examples of factors that we choose for analysis of percid communities are the size spectrum of available prey species, chosen in this context as a controlling factor, and light intensity, as a limiting factor. That is we propose to examine light intensity as a refugium generator and prey size as a rate controller, and we are primarily concerned with how these niche parameters differ among the constituent species of percid communities.

Prey size, a controlling factor — We earlier noted that net metabolic activity provides a basic common measure for contouring the niche hyperspaces of coexisting species. Net metabolism can be estimated directly, as with Fry's concept of "metabolic scope for activity" (Fry 1947), or indirectly, as one of the various dimensionless measures by which it is possible to estimate the efficiency of an activity that is common to all organisms in a community.

A convenient estimator, for present purposes, is the growth efficiency, K: the proportion of rations which is retained as new body substance ($\Delta W/R$). The relation of K to such variables as ration level and body size is fairly well understood for fishes (Paloheimo and Dickie 1966; Kerr 1971b): K is in fact a direct function of the metabolic scope for activity (Kerr 1971a). In brief, the growth efficiency of fishes, utilizing a prey resource of given "availability," varies inversely with fish size or its correlate, ration level. Beyond some low to intermediate level of "availability," the relationship is typically such that log K decreases linearly with increasing body weight, W. An "availability" is determined as some complex function of a variety of prey attributes (including prey size, abundance, motility, colouration, spatial and temporal vectoring, palatability, behavior, and associated olfactory and acoustical cues). It appears, however, that prey

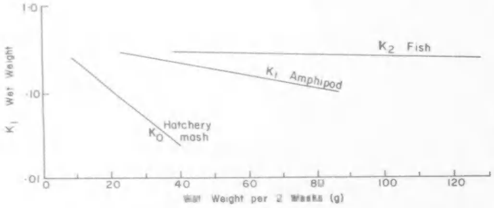

FIG. 2. The relation of growth efficiency K, to ration level for brook trout. The different K-lines result from differences in prey (particle) size. Adapted from Paloheimo and Dickie (1966).

size in itself is often a sufficient measure of availability for many analyses; we suppose this much in what follows. Figure 2 depicts the relations of K (the "K-lines") for brook trout feeding upon hatchery mash, *Gammarus*, and small fishes, that is, upon prey of increasing availability as measured by prey size. The inference (Kerr 1971b) is that predatory fishes can maintain a high level of growth efficiency if the prey resource permits sequential transfers to suitable K-lines as the predator grows. It follows that patterns of growth observed in natural communities must reflect the niche interactions associated with prey resource utilization.

As a demonstration, we derived relative measures of K for the four larger percid species that once were important to the Lake Erie fishery of the Laurentian Great Lakes: three *Stizosterion* taxa, *S. vitreum vitreum*, *S. vitreum glaucum*, and *S. canadense* (the last two subsequently became commercially extinct) and *Perca flavescens*, still a mainstay of the fishery. To obviate analyzing the presumably unstable period before the extinctions, we used growth data from an earlier period: Deason (1933) for *Stizostedion* spp., and Jobes (1952) for *Perca* sp. To make these calculations, we first converted Deason's length data to weight equivalents using $W = 0.0001\ L^3$ as a suitable approximation. We then calculated a relative K, using the expression $\Delta W/(W^{.85} + \Delta W)$, derived from the Winberg equation (Kerr 1971a) for the purpose, where W is body weight and ΔW the associated annual growth increment. The basis for this calculation and its associated qualifications is examined by Kerr (1971a, b) and is not repeated now; it is sufficient to note that this calculation is used here exclusively as a relative measure of growth efficiency.

The estimates for all four species (Fig. 3) fall on two K-lines, labeled K_1 and K_2. We infer that the two lines reflect the general diet types utilized at that time by Lake Erie percids of the given sizes. K_1 reflects the first transition diet, after the larval zooplanktivore stage, consisting of larger invertebrates and small species of fishes. K_2, achieved only by the walleye, *S. vitreum vitreum*, indicates the full piscivore habit. K_0, the planktivore K-line, does not appear in the figure because annual data were used and none of the predator species analyzed here remained an appreciable planktivore beyond its first year in Lake Erie.

Apart from the absence of the early planktivore phase, K_0, the K-lines depicted in Fig. 3 are similar to those in Fig. 2, and suggest the pervasive effects of prey size, itself a correlate of prey availability, in controlling the niches realized by these major components of the Lake Erie percid community. That is, prey size alone serves as a niche separator for the walleye at an early stage in its life cycle. Specifically, the separatrix occurs at a body size of 150–300 g, before the relative K of any of the four percids declines substantially.

On this basis, we conclude that the selected prey size, through its effects as a controlling factor within the niche hyperspace, operates as an important niche separator over much of the life history of the walleye. For those accustomed to thinking in such terms, we note that the transitions from K_0 to K_2 shown by the walleye can be compactly described as a sequence of elementary catastrophes (Thom 1975), with the underlying dynamics specified by appropriate metabolic equations (e.g. Kerr 1971b). It is clear that prey size alone cannot suffice in the present analysis to separate the niches of these four species, because only walleye (greater than 150 g) are separated by prey availability. For this reason, we now consider the effects of light as a limiting factor on the same group of species.

Light intensity, a limiting factor — In effect, we here invoke the limiting factors as a means of reducing the connectedness of community systems, thereby conferring the strong stabilizing effects for refugia deduced by Smith (1972). The effect we posit is precisely the opposite of a notion that engendered considerable interest until recently in the theoretical literature, namely, the idea that richly connected systems are more stable because of the greater number of alternative transfer pathways. Instead, we rely on the evidence against this conjecture (e.g. Gardner and Ashby 1970) to sustain our view that richly interactive systems lack strong stabilizing forces because of the absence of refugia, that is, in the absence of means to reduce the connectedness of the system.

We raise this evidence, for the same Lake Erie percids discussed earlier, in very simple terms: namely, by examining the qualitative effects of

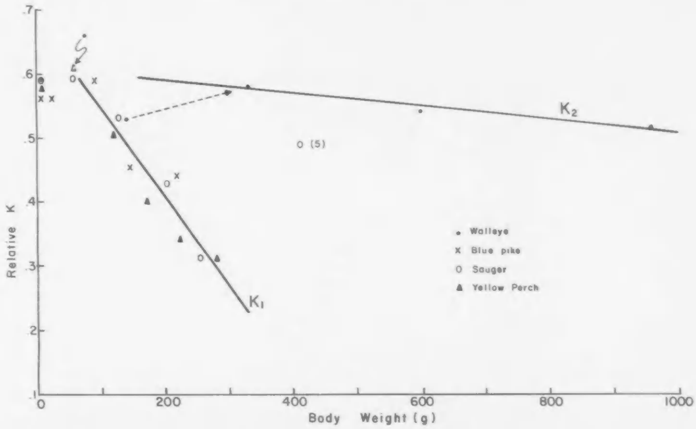

FIG. 3. Relative *K*-lines calculated from growth data for the four large percid species of Lake Erie (about 1920–50). The outlier for sauger, marked (5), is based on only five specimens and may be in error. The arrow indicates transfer of walleye from K_1 to K_2 efficiency lines. For explanation, method of calculation, and data sources, see text.

response to light intensity by the four percid species. In effect, we view light intensity response as a niche parameter which leads to stabilizing inhomogeneities, including spatial inhomogeneities. The effects we consider have been dealt with in detail elsewhere, especially in other papers in this symposium (Ryder 1977; Swenson 1977; Kelso and Ward 1977) and we are content here with noting the salient differences in very general terms. Thus, it is a reasonable approximation to assert that the light sensitivity of adult perch is small (*S*), that of walleye and blue pike (the two *vitreum* taxa) moderate (*M*), and that of the sauger (*S. canadense*) large (*L*). For the detailed effects of these light sensitivities, in terms of spatial segregation, feeding habits, and the like, we defer to the papers cited above; it suffices for our purposes to summarize these niche-separating effects by the notations *S*, *M*, and *L*.

Indeed, taken together with the effects of prey size as a controlling factor, which we denote here as *M* for species restricted to the K_1 efficiency line and *L* for the single species (walleye) with access to the K_2 growth efficiency line, we have now generated a sufficient basis for separation of the niche hyperspaces of the four species in question. To summarize, the niche differentiations for the four species are:

Species	Prey size	Light sensitivity
Perca flavescens	*M*	*S*
S. vitruem vitreum	*L*	*M*
S. vitreum glaucum	*M*	*M*
S. canadense	*M*	*L*

In association, the differences are sufficient to encapsulate the stabilizing inhomogeneities which sustained the complex percid community of Lake Erie.

Our purpose has been to describe the metabolic niche and provide a simple illustration of its use. The analysis provided here does not in itself reveal new information on percid community structure; it does illustrate the utility of the concept as a compact framework for analyses at the interface between autecology and synecology. Contouring the niche hyperspace in units of potential or realized metabolic scope for activity provides a unit of measure that is observable, common, and important to all organisms in a community. At the autecological level it facilitates quantitative comparisons, within or between communities, of the functional status of community components (taxa, or functional groups). At the synecological level it enables quantitative measures relevant to community properties, for example, the connectedness and interaction intensities which affect the persistence of interactive communities.

From the foregoing considerations, we conclude that fusion of the synecological niche definition of Hutchinson with the autecological concepts of Fry provides a conceptually satisfying and operationally tractable formulation of the ecological niche. Clearly, some troublesome problems remain to be resolved; but the metabolic niche embodied in the synthesis of the Hutchinson/Fry concepts provides a useful line of attack. In particular, a metabolic niche formulation is open to the conventional scientific methods of empirical investigation and evaluation; in our view, this transforms an appealing concept into an operational formulation. Whatever merit this construct has depends entirely upon its operational utility.

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Percids in Unperturbed Ecosystems[1]

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KELSO, J. R. M., AND T. B. BAGENAL. 1977. Percids in unperturbed ecosystems. J. Fish. Res. Board Can. 34: 1959–1963.

A review, primarily of papers from the PERCIS symposium, indicated that growth of percids in unperturbed ecosystems, which are rare and tend to be under harsh climatic regimes, was variable but tended to be low. Also, since growth appears to follow a clinal trend, heavily controlled by temperature, available data for unperturbed systems may not represent normal variation in growth. Recruitment did not appear to be a regular annual event and was adequately described by a wave pattern whose period was related to species longevity. Survival, therefore, was variable depending upon age-class structure of the community. Biomass, however, appeared to be a conservative property of unperturbed percid populations. Unperturbed populations should not be considered as ideal and we consider that preservation and study of unperturbed aquatic ecosystems can greatly increase understanding of the response of ecosystems to perturbation.

Key words: Percidae, unperturbed ecosystems, growth, recruitment, age-class structure, survival, biomass

KELSO, J. R. M., AND T. B. BAGENAL. 1977. Percids in unperturbed ecosystems. J. Fish. Res. Board Can. 34: 1959–1963.

Une revue, principalement des articles du colloque PERCIS, indique que la croissance des percidés dans des écosystèmes non dérangés, rares et tendant à se trouver sous des régimes climatiques durs, est variable mais généralement lente. En outre, comme la croissance semble suivre une tendance clinale, fortement contrôlée par la température, les données disponibles se rapportant aux systèmes non dérangés peuvent ne pas représenter la variation normale dans la croissance. Le recrutement ne semble pas être un événement annuel régulier, et on l'a décrit adéquatement comme une vague dont la période est liée à la longévité de l'espèce. La survie est donc variable selon la structure d'âge de la communauté. La biomasse, cependant, semble être une propriété conservatrice des populations non dérangées de percidés. Les populations non dérangées ne devraient pas être considérées comme idéales, et nous sommes d'avis que la préservation et l'étude d'écosystèmes aquatiques non dérangés peuvent nous aider grandement à mieux comprendre la réponse des écosystèmes à la perturbation.

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AQUATIC ecosystems undisturbed by man are rare and studies of them even rarer. Since man often imposes perturbations — e.g. cultural eutrophication, habitat modification, exploitation, and interactions imposed by introduction of exotic species — unperturbed ecosystems are usually remote and/or of limited value either economically or aesthetically. These systems therefore tend to be under harsh climatic conditions. Current unperturbed systems consequently may be atypical as a reference from which alterations imposed by perturbations can be evaluated.

In general, therefore, consideration of unper-

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turbed systems is unlikely to yield a single unequivocal baseline with which perturbation effects can be compared. Rather, each study of change should create its own benchmark. Nevertheless, we sought to develop generalities, where possible, for population characteristics of percids in systems having no exploitation, no exotic introductions, no cultural eutrophication, and no habitat modification.

Growth

Comparison of growth before and after perturbation is not a simple task. Growth rates themselves are generally difficult to derive and generalities difficult to ascertain. Yellow perch, *Perca flavescens*, growth depended upon both photoperiod and temperature (Huh et al. 1976) and, since days are longer in the north and warmer in the south, perch growth rates should theoretically be at a maximum in the middle of their range. However, the net effects of opposing factors seldom if ever balance. Nevertheless, temperature stands out as one of the most important abiotic factors influencing growth (Le Cren 1958; Coble 1966; Hokanson 1977) but a general growth rate applicable to all unperturbed populations cannot be identified. Colby et al. (1977) suggested a north–south cline in walleye (*Stizostedion vitreum vitreum*) growth rate which was considered to be primarily an effect of temperature and food availability. Furthermore, density-dependent effects, exploitation, year-class variation, food availability, and abiotic factors are known to influence growth in a variety of ways.

Eurasian perch, *Perca fluviatilis*, growth has been studied (Le Cren 1958; McCormack 1965) in two similar lakes in the English Lake District that were subjected to different degrees of exploitation and eutrophication. In Windermere, perch were heavily exploited from 1941 to 1947, then subjected to altered predation rates by manipulation of the northern pike population (Bagenal 1977) and exploited by sport fishermen, 1944 to present. In Ullswater, perch were only very lightly exploited up to 1942 and were not subjected to as much angling. Also, Ullswater did not contain northern pike and was less enriched. The two lakes are morphometrically similar and are within 15 km of each other. The differences in growth between the two populations are therefore most likely attributable to the different levels of exploitation and eutrophication. Mean lengths (cm) of perch back-calculated for the 1949 year-class in these two English lakes were:

	Females		Males	
Age	Windermere	Ullswater	Windermere	Ullswater
1	7.9	7.5	8.2	7.2
2	11.7	11.5	12.0	12.1
3	15.6	17.6	15.3	15.3
4	18.5	18.6	18.1	17.4
5	20.7	19.3	19.9	18.5
6	21.4	19.9	20.6	18.8
7	24.9	20.4	23.7	19.7
8	—	20.7	—	19.8
9	—	20.8	—	—

Although there was little difference between young fish, older Ullswater perch grew more slowly. Growth of perch in Windermere was linear whereas in Ullswater growth approximated the von Bertalanffy formula with an asymptote of 20.8 for the males and 21.8 for the females. Agreement with the von Bertalanffy equation was not necessarily a feature of unperturbed populations (Shafi and Maitland 1971; Craig 1974).

Atkinson (1910) transplanted tagged plaice, *Pleuronectes platessa*, from the unexploited fishing grounds in the Barents Sea, where they grew slowly, to the exploited grounds of the North Sea. These transplanted fish grew better than the local stock, indicating the plasticity and possible response of growth. It follows that genetic factors do not necessarily constrain the performance of unperturbed stocks. However, neither of the above cases was a satisfactory "before and after" perturbation comparison.

Recruitment and Age-Class Structure

In *Perca* sp., *Stizostedion lucioperca*, and walleye, recruitment was influenced by the strong and weak year-classes which passed through the population. These fluctuations occurred in unperturbed (Alm 1946; McCormack 1965; Kelso and Ward 1977) and perturbed (Bagenal 1977; Nagieć 1977; and others) systems. There is considerable evidence to suggest that in part year-class success may be associated with temperature either at certain times or throughout the period of growth. Other factors affecting recruitment of percids were predation, cannibalism, prey density, stock size, and water level fluctuations. Any perturbation affecting these is likely to alter recruitment.

Recruitment cannot be considered to be on a regular annual basis and Johnson's (1972, 1976) postulation that recruitment occurred in a wave fashion applied, with modification, to percids (Fig. 1). Recruited walleye in West Blue Lake (Kelso and Ward 1977) and Dexter Lake

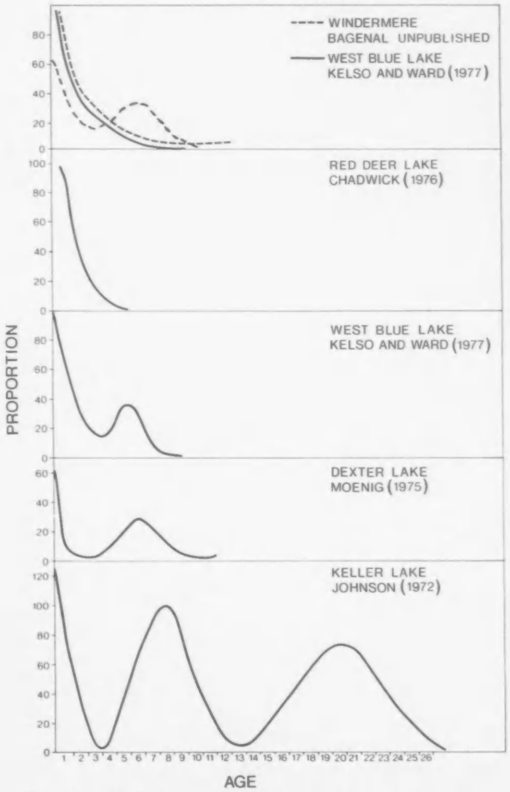

FIG. 1. Stylized pattern of age-class structure for percids in the form of the dynamic wave postulated by Johnson (1972, 1976). Since these are dynamic waves, the shape of the curves can vary and in fact assume virtually any of the shapes presented. Panels depict available data for perch (Windermere, West Blue Lake, and Red Deer Lake), walleye (West Blue Lake and Dexter Lake), and lake trout (Keller Lake).

(Moenig 1975) had a unimodal age-class structure with the peak followed by a regular decline in abundance (Fig. 1). For Eurasian perch in Sweden, Alm (1946) noted that certain year-classes dominated the population and, through cannibalism, restricted recruitment until that cohort had passed through the population, after which another strong, predominant year-class arose. This situation was also apparent in Ullswater but was less marked in the more perturbed Windermere over the same time period (McCormack 1965). Biologists through experience have come to expect unperturbed systems to possess fish communities having a preponderance of older individuals. Available data for unperturbed systems confirms that a wide range in age-class structure exists but also indicates that Johnson's waves can take a variety of shapes (Fig. 1) determined by population turnover rate. These waves pass through the population. Fishes of greater longevity probably have waves of longer period in the population while those having shorter life spans exhibit waves whose period varies with longevity as shown by the progression from the short-lived perch to the long-lived salmonid in Fig. 1. Thus, populations of walleye as well as perch (Chadwick 1976; Bagenal 1977) apparently reflected normal conditions of unperturbed populations and appeared to be adequately described by Johnson's (1972, 1976) wave hypothesis.

Survival

Few estimates of survival for unexploited populations exist but those available indicated great variation (Ricker 1947; Kennedy 1953), both between and within species. Undoubtedly survival, like growth, reflects a variety of influences of which population structure resulting from the variation in recruitment is an important factor. Survival in unperturbed percid populations is, owing to the variation possible in year-class structure, expected to be similarly variable. For this reason, survival rates estimated from consecutive year-class strengths must be used with caution.

For perch, the survival rate was 31% in Red Deer Lake (Chadwick 1976) and in Ullswater 44% for the 1949 year-class and 27% for the less numerous 1947 year-class. Unexpectedly, survival for the 1949 year-class was greater, 69%, in the more perturbed Windermere population (McCormack 1965).

For walleye, survival rates were 52% in Dexter Lake (Moenig 1975) and >20 <37% in West Blue Lake (Kelso and Ward 1977).

Healey (1975), in a review of unexploited whitefish populations, noted a wide range in survival, 20–80%, and both reinforced the range existing in unperturbed populations and recognized the problems associated with using estimates derived from year-class structure.

Biomass

Stability was apparent in biomass as shown by an instance in which biomass was examined during consecutive years (Kelso and Ward 1977). Conservancy of biomass in fish communities has not been tested per se; however, Johnson (1965) indicated that, with salmon, self-regulation in number occurred and was primarily attributable to mortality. Further, lightly exploited walleye lakes (Adams and Olver 1977) show little effect of exploitation and have continued yields at a similar level throughout their history. Conservancy of biomass, however, is not restricted to unperturbed systems as Regier and Hartman (1973), among others, have found stability in biomass in other, more perturbed ecosystems.

Production appeared characteristically low in unexploited systems as lowest available estimates for walleye production (Carlander 1977), 1.4 and 2.1 kg/ha, were from the only unperturbed populations that have been studied for this species. Chadwick (1976) also found very low production, all species including *Perca flavescens*, of 14.6 kg/ha, in unperturbed Red Deer Lake.

Obviously then, if fish populations naturally exhibit biomass stability, the interplay of age-class structure and biomass can result in a wide range of possible mortalities. For production of fish flesh, however, it must be remembered that low growth from the clinal trend of Colby et al. (1977) probably contributes to the low observed production in unperturbed systems.

General

For percids, stability in biomass appeared to exist. Further, although the populations were unperturbed, they were sensitive to biotic and abiotic influences. Year-class structure varied and strong/weak year-classes passed through the populations in the manner described by Johnson (1972, 1976). If we assume that biomass is a conservative property for unperturbed systems, variations should be about an equilibrium level and would be dampened by species longevity.

The consideration of these unperturbed percid populations has nullified, we hope, the concept that unperturbed systems are in some way more "ideal" for percids than unperturbed systems, depending of course upon the degree of perturbation. Further, this should serve as a cautionary note for those dealing with perturbations in that natural variability of certain properties of a fish community can be great. Our examination of unperturbed ecosystems has led us to the conclusion that preservation of unperturbed systems, particularly in favorable portions of the natural range, would greatly aid scientists' interpretive powers and could serve as testing grounds for hypotheses.

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Responses of Percid Fishes and Their Habitats to Eutrophication[1,2]

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Percid fishes are found in lakes that cover a wide range of trophic conditions. The responses of percids and their habitats to progressive cultural eutrophication are predictable. Alterations in physicochemical characteristics of habitats precipitate changes in phytoplankton, macrophytes, zooplankton, and benthos that are ultimately deleterious. Enrichment can lead to favorable responses in percids, but somewhere in the continuum of trophic conditions the responses become unfavorable. The relative level at which the response becomes negative varies with the species according to tolerances to altered environment, adaptabilities to new habitat and forage base, and reproductive behavior. Progressive eutrophication acts as a selective mechanism that leads to a predictable sequence of fish species. Other perturbations, such as exploitation and habitat modification, can act synergistically with cultural eutrophication in accelerating the sequence. As eutrophication proceeds, the succession of species may not lead to increased fish yield because part of the nutrient load may be channeled through unharvestable food chains.

Key words: Percidae, habitat, eutrophication, species dominance, food habits, parasitism, disease

LEACH, J. H., M. G. JOHNSON, J. R. M. KELSO, J. HARTMANN, W. NÜMANN, AND B. ENTZ. 1977. Responses of percid fishes and their habitats to eutrophication. J. Fish. Res. Board Can. 34: 1964–1971.

Les percidés se rencontrent dans les lacs couvrant une grande étendue de conditions trophiques. Il est possible de prédire les réponses des percidés et de leurs habitats à une eutrophisation culturale progressive. Les altérations aux caractéristiques physico-chimiques des habitats entraînent des changements dans le phytoplancton, les macrophytes, le zooplancton et le benthos, qui sont éventuellement nuisibles. L'enrichissement peut entraîner des réponses favorables chez les percidés, mais à un point quelconque du continuum de conditions trophiques, les réponses deviennent défavorables. Le niveau relatif auquel la réponse devient négative varie

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selon les espèces d'après la tolérance à un environnement modifié, l'adaptabilité à un nouvel habitat et à un nouveau fourrage, et le comportement reproducteur. L'eutrophisation progressive agit comme mécanisme de sélection entraînant une succession prévisible des espèces de poissons. D'autres perturbations, telles que l'exploitation et la modification de l'habitat, peuvent agir synergiquement avec l'eutrophisation culturale et accélérer la succession. A mesure que l'eutrophisation progresse, la succession des espèces peut ne pas entraîner d'augmentations du rendement en poisson, parce qu'une partie de la charge d'éléments nutritifs peut être canalisée dans des chaînes alimentaires non récoltables.

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THE responses of percid habitats and percid fishes to cultural enrichment are reviewed in this paper. Our observations are based on the sequences of events in a set of PERCIS lakes or embayments (hereinafter referred to as "PERCIS lakes") that cover a broad range of trophic conditions. The hypothesis examined may be stated simply as: The alteration of percid habitat through progressive eutrophication and subsequent changes in percid communities are predictable. In a continuum of trophic conditions, percid fishes respond favorably to increasing eutrophication and then unfavorably; the area in the trophic scale at which the response becomes negative varies with individual percid species.

Trophic Scale

The factors in productivity of lakes (climatic, morphometric, and edaphic) produce ultraoligotrophic conditions when each favors oligotrophy and hypereutrophic conditions when each favors eutrophy. Man's influence in producing cultural eutrophication is mainly in expanding the edaphic contribution, although climate and morphometry may also be changed by, for example, discharge of waste heat, water level fluctuations, and lakeshore modifications. The trophic state of a given lake is described by some point on a continuum between ultraoligotrophy (or harmonic oligotrophy, as described by Rawson 1956) and hypereutrophy. It is necessary, therefore, to determine the trophic state of a given lake in quantitative terms if responses by fish communities are to be compared among lakes. A variety of measures (Table 1) are available for this purpose (Vollenweider 1968; H. F. H. Dobson unpublished data). Some are causative, such as nutrient loading rates and nutrient concentrations (particularly at the time of spring mixing), whereas others are symptomatic, such as primary production rate, Secchi disc transparency, and oxygen depletion rate in the hypolimnion. In general, the trophic state, and especially the change in trophic state, should be assessed through the use of as many measures as possible.

The need for a variety of measures became apparent when we attempted to compare trophic status in the PERCIS lakes. Information on some measures was lacking, particularly for North American lakes. The data were most satisfactory for nutrient concentrations, Secchi disc transparencies, and the morphoedaphic index (MEI) (Ryder 1965). We used these measures, and others where information was available, to rank the PERCIS lakes in approximate order of trophic state (Table 2).

Effects of Eutrophication on Percid Habitats

Abiotic changes — The increased flow of nutrients into a water body leads to predictable responses in the abiotic and biotic components. As phytoplankton respond to enrichment through increased abundance and changes in species composition, color of the water may change and transparency decreases. The increased production of organic matter leads to an increase in deposition rate to sediments. Utilization of oxygen is accelerated, and depending on the oxygen reserve in the hypolimnion, which is largely determined by morphometric factors, anaerobiasis may occur. Nutrients may be released from the sediments during summer stagnation and distributed to the photic zone on overturn, or they may be released in shallow lakes by desorption from upper sediment layers ("aufgewirbelt") and dispersed through the photic zone by wind action. Other possible changes are decreases in pH and E_h (redox potential) and increases in alkalinity (in the hypolimnion), total dissolved solids, and decomposition products, such as carbon dioxide and hydrogen sulphide. The PERCIS lakes are not all eutrophic. Some are just beginning to show evidence of the eutrophication process (Lake of the Woods) and others have changed just recently from mesotrophy into a highly eutrophic state (Balaton). The most consistent changes (Table 2) are decreases in transparency and hypolimnetic oxygen and increases in nutrients and total dissolved solids.

Biotic changes — The most evident responses of phytoplankton to enrichment are increases in abundance and changes in species composition. The degree of response to cultural eutrophication appears to be related to the trophic condition of the lake before the addition of nutrients. Poorly buffered oligotrophic lakes usually show a greater

TABLE 1. Values of selected measures for various trophic states in PERCIS lakes.

Measure	Unit	Oligotrophic	Mesotrophic	Eutrophic	Hypereutrophic	References
Total P	$mg \cdot m^{-3}$	<9	9–18	18–50	>50	H. F. H. Dobson (unpublished data)
	Eutrophication potential: >10 $mg \cdot m^{-3}$ springtime assimilable P					
Total N	$mg \cdot m^{-3}$	<300	300–650	650–1500	>1500	Vollenweider (1968)
	Eutrophication potential: >300 $mg \cdot m^{-3}$ springtime assimilable N					
P loading rate	Eutrophication problem: $>.13\text{-}.5$ $g\ P \cdot m^{-2} \cdot yr^{-1}$			depends on depth and flushing rate		Vollenweider (1968)
N loading rate	Eutrophication problem: $>2\text{–}8$ $g\ N \cdot m^{-2} \cdot yr^{-1}$					Vollenweider (1968)
Primary production rate	$g\ C \cdot m^{-2} \cdot yr^{-1}$	<30	30–200	200–300	>300	Vinberg (1961)
Phytoplankton biomass	$cm^3 \cdot m^{-3}$	<3	3–5	5–10	>10	Vollenweider (1968)
Chlorophyll *a*	$mg \cdot m^{-3}$	<2.5	2.5–5	5–15	>15	H. F. H. Dobson (unpublished data)
Transparency (Secchi depth)	m	>6	6–3	3–1	<1	H. F. H. Dobson (unpublished data)
Hypolimnetic O_2 loss	$mg \cdot cm^{-2} \cdot mo^{-1}$	<0.5	0.5–1.0	>1.0		Hutchinson (1938)
Morphoedaphic Index	metric	<5.9	6.0–7.2	>7.3		Ryder (1965)
Organic matter in sediments	% dry wt	<16	16–30	>30		Entz (1977)

TABLE 2. Limnological responses in PERCIS lakes (ranked from most to least eutrophic) resulting from eutrophication. Symbols: N, nutrients (phosphorus and nitrogen); T, transparency; HO, hypolimnetic oxygen; TDS, total dissolved solids; P, phytoplankton; M, macrophytes; Z, zooplankton; B, benthos; +, increase; −, decrease; 0, no change; ( ), response in part of lake; blanks, information not available.

	N	T	HO	TDS	P	M	Z	B	References
Balaton	+	−		0	+	+ −	−		Entz (1977); Biró (1977); Herodek & Tamas (1975)
Bay of Quite	+	−	−		+	−	+	+	Hurley & Christie (1977)
Constance, lower	+	−	−	0	+	+ −	+	+	Hartmann & Nümann (1977)
Saginaw Bay	+	−	(−)	+	+				Eshenroder (1977); Beeton (1969)
Hjälmaren	+			+	+	+		+	Rundberg (1977)
Mälaren	+	−	−	+	+	+		(+)	Rundberg (1977)
Erie	+	−	(−)	+	+	−	+		Nepszy (1977); Leach & Nepszy (1976)
Green Bay	+	−	(−)	+				+	Beeton (1969); Howmiller & Beeton (1971)
Léman	+	−	−		+	−			Laurent (1972); J. C. Boyd & P. J. Laurent (unpublished)
Constance, upper	+	−	−	0	+	+	+	+	Hartmann & Nümann (1977)
SW Finnish lakes	+	−		+	+	+	+		Lind (1977)
Oneida			−					−	Forney (1977)
Ontario	+	−	(−)	+	+	+	+		Hurley & Christie (1977); W. J. Christie (pers. comm.)
St. Clair	+	−		(+)	(+)	0			Johnston (1977); Leach (1972)
L. of the Woods		−			+	+		−	Schupp & Macins (1977); Carlander (1942)

response to nutrient loadings than lakes naturally eutrophic. Shifts in species predominance, generally from diatoms and green algae to blue-green algae, indicate a transfer of energy to forms less suitable or accessible to most herbivores. Time and duration of algal blooms have been altered in some lakes (e.g. Lake Erie, Leach 1975; Lake Balaton, Herodek and Tamas 1975) by nutrient loading. In the Great Lakes there has been a gradual reduction in dissolved silica due to increased diatom production. Schelske and Stoermer (1971) have suggested that this depletion might lead to further shifts towards blue-green algae abundance.

In Lake Erie there has been a 20-fold increase in phytoplankton numbers in the past 50 yr (Leach and Nepszy 1976), and in Lake Constance average abundance increased ninefold between 1935 and 1970 (maxima more than 50-fold) (Hartmann and Nümann 1977). In Lake Balaton, between 1966 and 1973, abundance increased 12-fold (Herodek and Tamas 1975). In the lower section of the Bay of Quinte phytoplankton numbers increased about 17-fold between 1945 and 1972 (Hurley and Christie 1977).

The inshore areas, which are important habitats for percid species, are usually first affected by excessive phytoplankton production because nutrients are added there. In large deep lakes, thermal-bar effects enhance this process in spring.

During eutrophication, macrophyte production may increase in response to added nutrients or it may decrease in an advanced stage because of the shading effects of phytoplankton. Both responses were noted in Lake Constance by Hartmann and Nümann (1977) and in Lake Balaton

TABLE 3. Responses of fishes in PERCIS lakes (ranked from most to least eutrophic) in association with eutrophication. Symbols: +, positive response or changes in food habits, spawning habits, distribution, and species composition; −, negative response; 0, no response; ( ), response in part of lake; blanks, information not available.

					Distribution changes due to:			Biomass changes		Community changes	
	Growth rate	Food habits	Parasites & diseases	Spawning habits	Transparency	O_2	Food	Percids	Total fish	Species composition	% percids
Balaton	−	+		0	0	0	+	−	+	+	−
Bay of Quinte	+	+		+	+	+	+	0	+	+	0
Constance, lower								+	+	+	0
Saginaw Bay		+				+		−	+	+	−
Hjälmaren	+			0	0	0	0	+	+	+	+
Mälaren	+			+	+	+		+	+	+	+
Erie	+		+	+		+		+ − +	0	+	+ − +
Green Bay		+				+	+	−	+	+	−
Léman	+							+	+	+	+
Constance, upper	+	+	+	+			+	+	+	+	+
SW Finnish lakes	+								+	+	
Oneida		+				+		0	0	+	0
Ontario					+	+	+	+	0	+	+
St. Clair	0				0	0	0	0	0	+	0
Lake of the Woods			+		+					(+)	+?

by Entz (1977). Macrophyte stands increased in the upper lake of Lake Constance and decreased in the lower lake. Associated with the change in abundance was a shift to *Potamogeton pectinatus* from *P. perfoliatus* in the upper lake and a decrease in *Chara* sp. and *Elodea* sp. in both basins of Lake Constance. A similar decrease of *P. perfoliatus* and a parallel increase in *Stratiotes aloides*, *Trapa natans*, and *Elodea canadensis* occurred in Lake Balaton. In the Bay of Quinte, reduced water transparency has greatly decreased abundance and species diversity of macrophytes (Hurley and Christie 1977).

The responses of zooplankton to eutrophication are not entirely clear, largely because effects can be masked by selective feeding of changing populations of fishes (Brooks 1969; Wells 1970). There were indications in some of the PERCIS lakes that abundance and/or species composition had changed. In the upper Lake Constance the abundance of planktonic crustaceans has increased thirteenfold and the numbers of species has almost doubled since before eutrophication (Hartmann and Nümann 1977). Moreover, several zooplankters previously considered as littoral extended their habitat range to the limnetic zone. Abundance also increased in the upper Bay of Quinte (Hurley and Christie 1977) and in Lake Erie (Leach and Nepszy 1976). On the other hand, Entz (1977) recorded a decrease in abundance in Lake Balaton, particularly for copepods.

Much of the increased energy generated by eutrophication is deposited in lake sediments, where it is available to the benthic community. This loading of organic matter may be beneficial to some species, but when it is heavy enough to alter the physical–chemical system it can lead to extensive changes in the taxonomic composition of the community. The decline in numbers and diversity of pollution-intolerant species and the increase in abundance of pollution-tolerant species have been documented (Carr and Hiltunen 1965) for Lake Erie, where mean loadings of organic carbon have increased fivefold since 1850 (Kemp et al. 1974). As eutrophication proceeds the shift in species appears to be generally from larger benthic organisms (e.g. *Hexagenia* spp.) to smaller forms (e.g. chironomids, oligochaetes). Tubificids in the upper lake of Lake Constance have increased more than 50-fold since before eutrophication (Hartmann and Nümann 1977). In the Bay of Quinte the species composition of benthic communities was related to degree of eutrophy and water temperature (Hurley and Christie 1977). Alteration of the benthic community and increases in abundance have been recorded (Grimås et al. 1972) for Lakes Mälaren and Hjälmaren in Sweden.

Responses of Percids to Eutrophication

Percid fishes responded to eutrophication in PERCIS lakes in characteristic ways. Growth increased to some threshold level and then decreased, parasitism increased, food habits, distribution, and spawning habits were altered and percid biomass increased to some threshold level and then decreased. However, some PERCIS lakes were exposed to additional perturbations such as exploitation, habitat modification, and introduction of exotic species, and delineation of responses due entirely to eutrophication was not always possible. The responses of percids in the PERCIS lakes are summarized in Table 3.

Growth — Walleye (*Stizostedion vitreum vitreum*), pikeperch (*S. lucioperca*), and Eurasian perch (*Perca fluviatilis*) responded to increased eutrophication with an increase in growth rate for young and/or adults in Lakes Erie, Hjälmaren, Mälaren, Constance, and Léman. Although growth for most percids generally increases with progressive eutrophication, Lake Balaton, where growth of pikeperch has decreased since the 1950s (Biró 1977), demonstrates that the process is not continuous and that some maximum within the trophic continuum exists. It is sometimes difficult to attribute growth rate changes to eutrophication alone and not also to exploitation or other factors affecting density (Wiener and Fuller 1975), but there is sufficient evidence in the histories of the PERCIS lakes and in the literature (Haines 1973; Marciak 1975) to implicate eutrophication as a major factor in growth response.

Parasitism and diseases — Hartmann and Nümann (1977) reported an increased infestation of Eurasian perch by *Diplostomum* sp., a parasite which causes hematoma of internal organs and early summer mortality of adults. Increases in *Diplostomum* sp. and other parasites have been attributed to increases in vegetation and snails in response to acceleration of eutrophication. Dechtiar (1972) reported an increase in the number of species of fish parasites in Lake Erie and suggested that, in part, these resulted from changes in environment and fish fauna. In a comprehensive review of fish parasitology, Dogiel et al. (1970) suggested that the incidence of parasitism in fishes increases with eutrophy.

In Lake of the Woods the incidence of *Lymphocystis* sp. in walleyes was greater in eutrophic areas such as Sabaskong Bay than in the mesotrophic northern sector (Schupp and Macins 1977). Snieszko (1974) suspected that the incidence of infectious diseases in fish is related to stress caused by eutrophication, pollution, pesticides, and temperature but stated that the processes involved in the relationships are not well understood.

Food habits — The shift in benthic species from larger to smaller forms can affect the diet of fishes. The loss of *Hexagenia* spp. from the diet of percids has been widespread (Lake Erie, Bay of Quinte, Green Bay, Saginaw Bay, and Oneida Lake). In Lake Constance the progression from large to small items in the diet of percids was confirmed by Hartmann and Nümann (1977). In Lake Balaton chironomids have replaced larger benthic food items such as amphipods (Biró 1977).

Distribution — Decreasing transparency and changes in the oxygen regime and invertebrate community can influence distribution of percids. Periodic and regular oxygen depletions in the western and central basins of Lake Erie have apparently caused migrations of blue pike (*S. vitreum glaucum*) and walleye (Regier et al. 1969). Oxygen deficits have also affected distribution of percids in Lake Mälaren (Rundberg 1977), Oneida Lake (Forney 1977), Saginaw Bay, and Green Bay (Schneider and Leach 1977). Decreasing transparency apparently favored sauger (*S. canadense*) in Lake Erie (Leach and Nepszy 1976) and in Lake of the Woods (Schupp and Macins 1977). Responses to turbidity are species specific, since reaction of percids to light is not consistent for all species (Ali and Anctil 1977). Distribution of percids has changed, primarily in response to availability of food, in Lake Constance (Hartmann and Nümann 1977) and Lake Ontario (W. J. Christie personal communication). In Lake Constance, Eurasian perch has become progressively more pelagic in response to increased abundance of zooplankton. In Lake Ontario, yellow perch (*P. flavescens*) has expanded its range in littoral areas, although this change may have resulted from food availability, preferred light, or population pressure.

Spawning habits — Eutrophication has altered time of spawning of Eurasian perch in Lake Constance (Hartmann and Nümann 1977), but the major effect on percid reproduction has been loss of spawning areas. As eutrophication progressed in Lake Mälaren pikeperch gradually moved to deeper water to spawn (Rundberg 1977). In the Bay of Quinte, walleye spawned in the lower reaches of tributaries and along rocky shores of the bay, but are now observed (W. J. Christie personal communication) to be spawning in the streams only, probably because organic matter deposition or littoral algae have rendered the shoals unsuitable. In western Lake Erie the spawning reefs are sometimes unsuitable for walleye spawning (depending on wind conditions) because of deposition of organic matter. There also are cases where tributary spawning has been curtailed, for example, in Saginaw Bay, Green Bay, and Lake Erie, but the effects of damming, siltation and, industrial pollution probably exceeded those of eutrophication.

Species predominance — The expected sequence in fish species associated with progressive eutrophication has been described by Colby et al. (1972), largely from observations on salmonines and coregonines. Hartmann (1977) demonstrated a succession in fish yields in relation to eutrophication for 17 European lakes (Fig. 1). The data on species changes in the PERCIS lakes reinforce their models. A change in total species composition was observed in all of the PERCIS lakes (Table 3). The percentage of percids in the

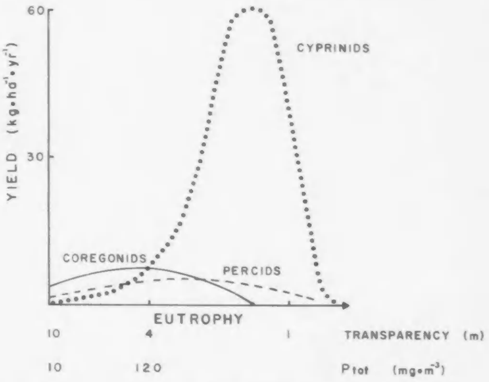

FIG. 1. Summary of relations between increasing eutrophy and yields of corregonids, percids, and cyprinids for 17 European lakes (from Hartmann 1977).

community increased in seven lakes and decreased in three.

Percid species usually benefit from increasing eutrophication, perhaps because of reduced competition and predation and enhanced food supply. In general, the biomass of percids increased in those lakes where the percentage of percid species in the community was expanding. However, Lake Balaton, which is the most eutrophic lake in the set, experienced declines in percid biomass and percentage composition in the community. Eurasian perch has almost disappeared from Lake Balaton and the stock of ruffe (*Gymnocephalus cernua*) has decreased (Biró 1977). Growth rate of pikeperch has decreased and Biró (1977) considers that the present state of eutrophication in Balaton is not favorable for this species. The stock of cyprinids, particularly bream (*Abramis brama*), is increasing. The growth rate of bream is also increasing, apparently in response to the accelerated eutrophication. In Saginaw Bay, nutrient loading has been implicated in the decline of walleye (Schneider and Leach 1977) and yellow perch (Eshenroder 1977). In southern Green Bay, eutrophication probably contributed to the decline of walleye (Schneider and Leach 1977).

General Discussion

It has been demonstrated in the PERCIS lakes that percid fishes generally respond to increasing eutrophy in a predictable way. In early stages of the enrichment process, the increased productivity of the system is reflected in increased growth rate and production of percids. As the process continues, less tolerant competitors and predators may be removed, causing a further shift towards percid production. In large lakes this process occurs first in shallow basins and embayments.

The process is not continuous and somewhere along the trophic continuum (depending on lake morphology, flushing rate, etc.), individual percid species begin to respond unfavorably to progressive eutrophication (Fig. 2). The level in the trophic scale at which the response becomes negative appears to vary among species. We suggest that the order of percid species from least to most tolerant of the detrimental effects of eutrophication may be sauger, walleye, perch species, ruffe, and pikeperch. In North American PERCIS lakes, sauger appeared to be affected adversely before walleye and walleye before yellow perch. In the Great Lakes, sauger stocks usually declined before walleye, which in turn declined before yellow perch (Schneider and Leach 1977; Johnston 1977). In Lakes Erie and Ontario the blue pike declined after sauger and before walleye (Smith 1972). In European PERCIS lakes, ruffe has demonstrated more ability to withstand the unfavorable effects of eutrophication than Eurasian perch and on a relative basis, pikeperch appear to be more successful than ruffe. Lind (1977) has shown that pikeperch is more successful than Eurasian perch in eutrophic lakes in southwestern Finland. Rundberg (1977) concluded that eutrophication has favored pikeperch in Lakes Mälaren and Hjälmaren in Sweden, whereas Eurasian perch has declined because of eutrophication and/or competition from the more successful pikeperch. In Lake Balaton, where Eurasian perch has virtually disappeared, the ruffe stock is decreasing and pikeperch is beginning to show indications of stress from eutrophication and competition from cyprinids (Biró 1977). However, our views on the sequence of species are general and partly speculative because of the presence of other perturbations.

Some factors which contribute to the variation in success of percid species in withstanding progressive eutrophication are (a) ability to readily change distribution patterns when preferred habitat becomes unsuitable, (b) ability to switch to alternative prey when favored food organisms are lost, and (c) reproductive behavior. We consider that variation in reproductive habits may account for a major part of the differences in ability of percid species to tolerate eutrophic conditions. Tributary-spawning stocks of sauger and walleye are more vulnerable to loss of spawning habitat than lake-spawning stocks. Lake-spawning sauger and walleye broadcast their eggs on the bottom, where survival may be poor if enrichment has led to heavy sedimentation of organic matter. On the

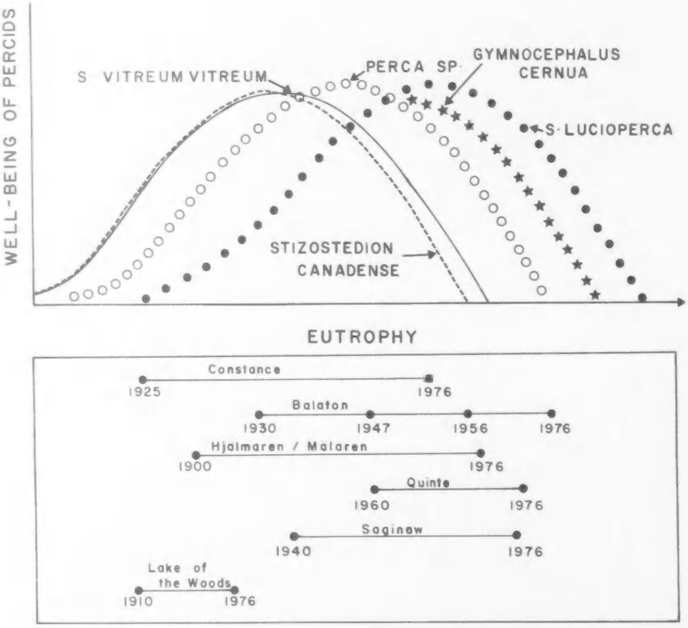

FIG. 2. Hypothetical relations between well-being of percids and increasing eutrophy. Estimated historical and present positions on the trophic continuum are shown for selected European and North American PERCIS lakes.

other hand, perch species release eggs in ribbons which although attached to the bottom, float upwards or become entangled on submerged plants and debris, ensuring aeration even if conditions at the mud–water interface are unsuitable. Of the percid species, the pikeperch appears to have the best mode of reproduction for survival in eutrophic conditions. Males build nests on suitable substratum, "fan" the eggs, and guard the brood. Therefore, the pikeperch gains a survival advantage over other percid species in a eutrophic environment.

The data on PERCIS lakes support the inferences of Colby et al. (1972) and Hartmann (1977) concerning the relation between species succession and increasing productivity of waters. The data indicate that if the vulnerabilities and tolerances of fishes are known, the sequence of species selected by eutrophication can be predicted. The pressures exerted by additional perturbations, such as exploitation and habitat modification, generally accelerate the selection process. There is some evidence (Bonar 1977; Loftus 1976) that the succession of species brought about through cultural eutrophication does not necessarily lead to an increase in fishing yield. Some of the additional nutrients may flow through energy systems inaccessible to or not utilized by harvestable species. These processes have obvious implications in the management of enriched lakes for optimum total yield and in the rehabilitation of lakes for the production of desirable species and therefore, warrant further elucidation.

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A Dynamic Model of the Western Lake Erie Walleye (*Stizostedion vitreum vitreum*) Population[1]

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SHUTER, B. J., AND J. F. KOONCE. 1977. A dynamic model of the Western Lake Erie walleye (*Stizostedion vitreum vitreum*) population. J. Fish. Res. Board Can. 34: 1972–1982.

A simple population model of western Lake Erie walleye was constructed using empirical relationships linking growth to population density and recruitment to breeding stock size and the spring water temperature regime. Given a reasonable set of values for annual rates of natural and fishing mortalities, consistent with empirical estimates of total survival for the period from 1947 to 1975, the model generated a pattern of behaviour similar, both qualitatively and quantitatively, to that exhibited by the real population. Two types of stochastic model, based on the initial population model, were used to derive optimal harvest strategies for the population. Optimal strategies were not sensitive to variations in catchability and natural mortality. Yields produced were highly sensitive to variations in both these factors. A refined and extended version of this model may serve as a useful tool in developing realistic management policies for this population.

Key words: Percidae, dynamic model, population model, *Stizostedion*, Lake Erie walleye, growth, density, survival, management implication

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Les auteurs ont construit un modèle simple de population de dorés jaunes du lac Erié occidental, utilisant des relations empiriques reliant la croissance à la densité de population d'une part, et le recrutement à la taille de stock reproducteur à la température de l'eau au printemps d'autre part. Avec une série raisonnable de valeurs de taux annuels de mortalité naturelle et due à la pêche, conformes aux estimés empiriques de survie totale pour la période de 1947 à 1975, le modèle engendre un comportement semblable, à la fois qualitatif et quantitatif, à celui que montre la population réelle. Deux types de modèles stochastiques fondés sur le modèle de population initial, ont été utilisés pour déduire des stratégies de récolte optimale pour la population. Les stratégies optimales ne sont pas sensibles au variations de vulnérabilité à la capture et de mortalité naturelle. Les rendements obtenus sont très sensibles aux variations de ces deux facteurs. Une version raffinée et élargie de ce modèle peut être un outil utile dans le développement de politiques de gestion réalistes pour cette population.

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FOR well over a century, the western Lake Erie walleye population has been subjected to a variety of anthropogenic stresses. By the late 1940s progressive destruction of inshore spawning areas had led to the predominance of the offshore spawning grounds (Hartmann 1973; Leach and Nepszy 1976). This in turn has resulted in a strong dependence of year-class strength on the rate of water temperature increase over the spawning reefs during the spring (Busch et al. 1975). In addition, a significant increase in the exploitation rate in the early 1950s led to a rapid increase in the annual commercial catch. Beginning in 1950 at a value of 2.6×10^6 kg, it rose rapidly to an extreme peak of 7×10^6 kg in 1956, declined precipitously to $<0.5 \times 10^6$ kg in 1961 and remained low until 1970, when the fishery was closed due to mercury contamination. These variations in catch were accompanied by a progressive decline in catch per unit effort and year-class strength (Parsons 1970; Regier et al.

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1969), a truncation of the age distribution (Busch et al. 1975; Parsons 1970), and a progressive increase in length at age (Parsons 1970). In the years following the ban on commercial fishing, most of these trends have reversed.

Among the recent authors (Busch et al. 1975; Hartmann 1973; Nepszy 1977) who have reviewed the history of this population, there is general agreement that the rate of exploitation reached nonsustainable levels sometime in the mid-1950s and that this was a primary cause of many of the changes listed above. Combining this interpretation of events with the known dependence of year-class strength on the spring warming rate leads to a rather simple qualitative model of the population consisting of a standard, hump-shaped stock–recruitment relationship, modified by the influence of the spring warming rate; a negative relationship between growth rate and population size, offset by a positive relationship between growth rate and forage density. In this paper, we attempt to carry out the following objectives: evaluate the data base for the population to determine if sufficient information exists to derive quantitative estimates of these basic relationships; incorporate the estimated relationships into a quantitative dynamic model of the population and determine if its behavior is consistent with observed behavior; explore some of the ways such a quantitative model could be used as a tool in managing the population.

Data Base: Sources and Preliminary Manipulations

The character and origins of the data base are outlined in Table 1. Details of the analyses summarized below can be found in Shuter and Koonce (1976), copies of which are available from the senior author.

Trap net catches per unit of effort (CPE) from United States waters (Kutkuhn et al. 1976; Parsons 1970; Regier et al. 1969) were assumed to provide the most reliable information on long-term changes in population size. Annual fall CPE (kilograms per lift) values from the late 1940s to 1969 are available, or can be estimated, for Ohio and Michigan waters. Concurrent information on the age distributions and mean weights per fish is also available. From these data, we derived separate sets of abundance indices (number per lift) for age-groups 1 through 4, as well as for all fish age 1 and over, from the Ohio and Michigan data for the periods 1948–69 and 1946–69, respectively.

For 1947–1969 separate estimates of the total annual survival rate for each of the age-groups 2–4 were derived from the two sets of abundance indices. Concurrent estimates were then averaged and variations over time smoothed, using 3-yr running averages, to give the values presented in Fig. 1. An upper limit of 80% was imposed to conform with the estimated annual natural mortality rate of 20% (Kutkuhn et al. 1976).

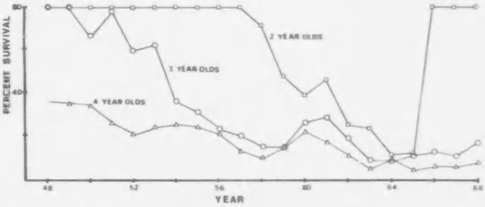

FIG. 1. Yearly survival rates for age groups 2 through 4, obtained by averaging independent estimates from Michigan and Ohio abundance data and then smoothing, using 3-yr running averages.

Since 1-yr-old fish were not fully recruited to the trap net fishery in the years before 1958 and after 1965 (Busch et al. 1975; Parsons 1970), the abundance indices for this age-group were negatively biased, leading to anomalously high 2-yr-old survival estimates for these time periods. The 2-yr-old indices for the years before 1953 had a similar bias. For those years where the 1-yr-old index was biased but the 2-yr-old index for the same year-class was unbiased, corrected indices were derived as follows:

$$\text{corrected } I_1{}^i = I_2{}^{i+1} \Big/ \left(\frac{\phi_2{}^{i+1} + \phi_3{}^{i+1}}{2}\right)$$

where $I_j{}^i$ is the observed fall abundance for age j fish in year i and $\phi_j{}^i$ is the estimated survival rate for age j fish in year i, as given in Fig. 1. Applying this and similar procedures to the indices derived from Michigan data, we developed a complete set of corrected abundance indices for all numerically significant age-groups for 1946–68.

In addition to the population statistics calculated above, the spring rate of water temperature increase in the area of the major spawning reefs was determined for each year from 1918 to 1974. Following Busch et al. (1975), a least squares linear regression was used to estimate the average rate of warming from the daily mean temperatures for April 6 through May 15, an interval that consistently included the major walleye spawning period. Estimates were approximately normally distributed with a mean of 0.215 deg C/day and a SD of 0.069.

Stock–Recruitment Relations

To investigate the form of the stock-recruitment relationship, annual indices of breeding stock size and year-class strength were derived for 1947–67.

In 1927, about 40% of 3-yr-old fish were mature (Deason 1933). Length at a given age was similar to that noted in 1947 (Lawler 1948). By 1965, the percentage of mature 3 yr olds had increased to over 80% (Wolfert 1969). Throughout this period most fish age 4 and over were mature. This shift in the average age at maturity was accompanied by a

TABLE 1. Types and sources of primary data sets relating to western Lake Erie walleye (*Stizostedion vitreum vitreum*).

Information	Time period	Sources
Catch and effort data by gear, statistical district, year, and season	1939–69[a]	Regier et al. (1969, unpublished data) Kutkuhn et al. (1976)
Age compositions of commercial catches by gear, statistical district, year and season	1943–70[a]	Busch et al. (1975), Parsons (1970), Kutkuhn et al. (1976)
Mean weights of fish in fall trap net catches	1943–62	Parsons (1970)
Young-of-the-year catch indices	1959–75	Kutkuhn et al. (1976)
Lengths at various ages	1920–67[a]	Adamstone (1922), Deason (1933), Lawler (1948), Parsons (1970, 1972), Wolfert (1972)
Weights at various ages	1962–66	Regier et al. (1969), Kutkuhn et al. (1976)
Lengths and ages at maturity	1927–66[a]	Deason (1933), Wolfert (1969)
Spring water temperatures	1918–74[a]	Anon. (1961), Ohio Dep. Nat. Res. (unpublished data)

[a] Time series incomplete.

marked increase in length at age and a moderate increase in length at maturity. By assuming that these events were related and occurred in concert (Hile 1954; Wolfert 1969), yearly estimates of the percentage of spawners that were 3 yr olds were derived from data on the length of 2 yr olds in the fall. In addition, the spring abundance of fish age 3 and over in a given year was found to be highly correlated with both the fall abundance of fish age 3 and over in the same year and the fall abundance of fish age 2 and over in the previous year. On the basis of this result, two independent indices of breeding-stock size were derived for each year using the appropriate estimates for the percentage of spawners that were 3 yr olds, the fall abundance of fish age 3 and over and the fall abundance of fish age 2 and over.

In recent years, estimates of the density of young-of-the-year walleye (YOY index catches) in the fall have served as useful measures of recruitment to the fishery by individual year-classes (Busch et al. 1975), indicating that year-class strength is generally set by the end of the first growing season. Unfortunately, values for this index were available only for 1959–75. Values of the fall abundance index for 1 yr olds were available for all year-classes from 1945 to 1967. In addition, these values were highly correlated with the YOY index catches ($r = 0.89$ for year-classes 1959–67) and Parsons' (1970) virtual population estimates of year class strength ($r = 0.863$ for year-classes 1945–61). Therefore we concluded that the 1-yr-old abundance indices were a reliable measure of recruitment to the population.

After converting the recruitment and stock size indices to logarithms, stepwise multiple regression analyses were performed to estimate the relationships linking recruitment to breeding-stock size and the rate of water temperature increase in the spring. A separate analysis was carried out for each of the two indices of breeding stock size available. The two analyses produced similar results (see Table 2): a strong dependence of recruitment on stock size and the spring rate of warming. In the relations between recruitment and stock size, the slope decreased monotonically to zero with increasing stock size, indicating that we were dealing with the left half of a typical, hump-shaped stock–recruitment curve. The temperature effect was multiplicative and independent of stock size. This is in accord with Ricker's (1975) general analysis of the probable effects of physical environmental factors on recruitment.

A single expression linking the number of yearlings in the spring of one year to the number of mature fish and the spring water temperature regime of the previous year was obtained from the results in Table 2 by averaging the estimates for each parameter, adjusting the constant term to convert the expression to a predictor of the arithmetic mean of the recruit-

TABLE 2. Results of multiple regression analyses of the relationship linking recruitment (R) to breeding stock size (S) and the rate of water temperature increase in the spring (ΔT) using stock size indices based on the fall abundance of fish age 3 and over (I_{3+}) and on the fall abundance of fish age 2 and over (I_{2+}).

Multiple r	Fitted parameters (+ SD): log R = $\alpha + \beta \log S + \delta \Delta T$ α	β	δ
I_{3+}			
0.837	0.009 (0.28)	0.488 (0.09)	4.016 (1.23)
I_{2+}			
0.804	−.42 (0.32)	0.53 (0.11)	4.422 (1.35)

ment index (Ricker 1975), adjusting for the effects of summer natural mortality on 1-yr-olds assuming an annual natural mortality rate of 20% (Kutkuhn et al. 1976), and converting the relative abundance indices for recruitment and stock size to absolute numbers via a conversion factor of 115,400 fish per index unit — a value obtained by assuming an average population size of 1.5×10^6 fish aged 1.5 yr or over for 1963–69 (Kutkuhn et al. 1976). The resultant expression was;

$$R = 325S^{0.505}[15850]^{\Delta T} \qquad (1)$$

where R is the number of yearlings in the spring of year i, S is the number of mature fish in the spring of year $i - 1$, and ΔT is the rate of water temperature increase (degrees Celsius per day) in the spring of year $i - 1$.

It should be noted that stock size and recruitment followed similar secular trends. Therefore the strong correlation between these two variables may have stemmed, not from a causal connection, but rather from the action of some additional factor operating to reduce each of the variables over approximately the same time frame. Given the available data, we cannot definitively reject this possibility. However, the following results provided some support for the causal interpretation.

After converting to logarithms, third-degree polynomials were fitted to the recruitment and stock size data to remove the secular trends. Multiple regression analyses were then repeated using the deviations of recruitment and stock size from the fitted trend lines. In both analyses, a positive stock effect was still detectable and the fitted values for both the stock and temperature coefficients were roughly comparable to those in Table 2. Using a different approach, each data set was divided into two groups: one covering the year classes from 1947 to 1956, the other covering those from 1958 to 1967. Separate log-log regressions of recruitment on stock size were calculated within each group, and in both, a positive stock effect on recruitment was detected. These slope estimates were roughly similar in value to each other and to the corresponding estimate in Table 2. All of these results support the view that a stable stock recruitment relationship was operative in this population over the period from 1947 to 1967.

Relations Between Growth Rate and Population Density

Implicit in the qualitative model outlined in the introduction is the assumption that the observed trend in growth rate was caused by a gradual reduction in intraspecific competition for food. Detailed elaboration of such a relationship would require concurrent information on forage and population density. Since extensive information on forage density was not available, we restricted our analysis to an attempt to relate growth rate to population density.

In Fig. 2 the total length after four growing seasons for each year-class from 1947 to 1963 (Parsons 1970; Wolfert 1972) is plotted against the abundance index of fish age 1 and over for the year when the year-class was hatched. The relation between these two quantities is adequately described by the equation

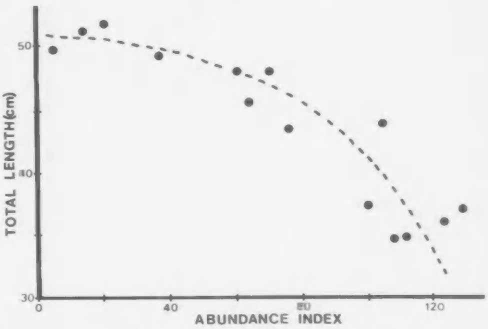

FIG. 2. Relation between total length after four growing seasons, for year-classes from 1947 to 1963, and the abundance index (number fish per trap net lift) for fish age 1 and over in the year when the year-class was hatched.

$$L_4 = 51.6 - 0.673\, e^{.027 I_{1+}}$$

where L_4 is the total length (centimetres) after four growing seasons and I_{1+} is the abundance index for fish age 1 and over in the year when the year-class was hatched. This relationship was derived from a log-log regression of $(L_4 - 51.6)$ on I_{1+}. Converting the equation to absolute units using the abundance index conversion factor given in the previous section yields

$$L_4 = 51.6 - 0.673 \times e^{(.23 \times 10^{-6})(\text{no. fish aged } 1+)} \qquad (2)$$

Since this relationship can be used to predict the average length in a year-class after four growing seasons, all that is now required is a means of predicting the length at other ages from the length at age 4. The total lengths at various ages given by Adamstone (1922), Deason (1933), Lawler (1948), Parsons (1972), and Wolfert (1972) all conform rather closely to the equation

$$L_{t+1} = 12.4 + .836L_t \qquad (3)$$

where L_t is total length (centimetres) at age t and L_{t+1} is total length 1 yr later. This relationship, or its inverse, can then be used in conjunction with equation 2 to predict variations in length at any age from variations in population density. Variations in weight can be predicted from variations in length using the length–weight relationship for western Lake Erie walleye by Baker et al. (1976):

$$W = 1.32 \times 10^{-2} L^{2.9302} \qquad (4)$$

where W is weight in grams and L is total length in centimetres.

Structure and Behavior of the Population Model

The relationships 1 through 4, given in the previous sections, form the heart of the model population. Age-groups 1 through 8 are represented explicitly, with a constant annual natural mortality rate of 20% (Kutkuhn et al. 1976) imposed on each group. A minimum length at age 1 equivalent to the minimum observed length (15.2 cm, Deason 1933) during 1927–66 is also imposed on the model. Known changes in the age at maturity are accounted for in the manner outlined earlier. The total fishing mortality for each year is assumed to occur all at once halfway through the growing season.

The behavior of the model was compared with that of the real population for 1947–75. Initial population size in the spring of 1947 was estimated from the fall abundance indices for 1946 and 1947. Three annual survival rate schedules, A through C, were used. In all three, the survival rates of fish age 4 and over for 1947 through 1969 were taken from the estimates for 4 yr olds given in Fig. 1 (1947 and 1969 values assumed equal to 1948 and 1968 values, respectively). Values for 1970 to 1975 were taken from Kutkuhn et al. (1976). Recognizing the known positive bias in the survival estimates for 2 and 3 yr olds in some years, we assumed that the actual survival rates for each of the age-groups from 1 through 3 were bounded above by the estimates given for the group in Fig. 1 and bounded below by the estimates for fish age 4 and over. An upper bound of 80%, corresponding to the action of natural mortality alone, was assigned to the 1-yr-old survival rates. In general, the values in schedule A were chosen from the upper regions of their respective ranges, and the corresponding values in schedule B from the lower regions.

The simulated catches produced by schedules A and B bracket the observed catches (Fig. 3). Under A the simulated catch peaks later than the observed catch and then declines to an average level considerably higher than that observed. Under B the simulated catch peaks earlier and at a lower level. It then declines to an average level only slightly higher than that observed. These results suggest that up until the mid-1950s the schedule B survival rates are somewhat lower than those experienced by the real population, whereas from the mid-1950s to the end of the 1960s the schedule A survival rates are somewhat higher.

Schedule C (Fig. 4) was constructed with this interpretation in mind. From 1947 to 1953 survival rates similar to those in A are used. From 1954 to 1956 there is a transition to a set of rates similar to those in B, which then continue in effect until 1975. These trends in survival rate are consistent with the following sequence of events. In the early 1950s an increase in the use of small- and large-mesh gill nets, a decrease in the minimum size limit in Canadian waters, and a steady increase in growth rate led to a rapid increase in fishing mortality, particularly among younger fish (Busch et al. 1975; Regier et al. 1969). Beginning in 1966 increases in (Busch et

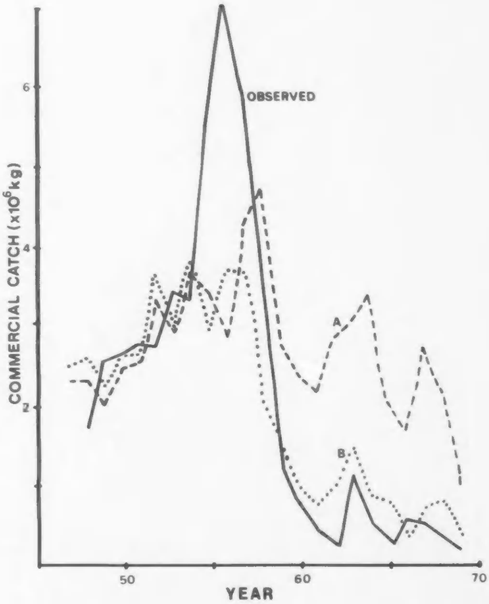

FIG. 3. A comparison of observed commercial fishery catches with catches generated by the model using survival rate schedules A and B. The derivation of these schedules is given in the text.

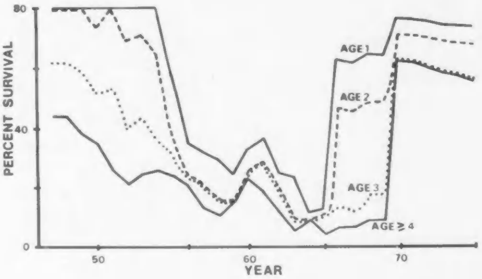

FIG. 4. The annual survival rates, by age-groups, used in survival rate schedule *C*. The derivation of these values is given in the text.

al. 1975) and enforcement of (Regier et al. 1969) minimum size limits led to a reduction in the fishing mortality rates on younger fish. This age-dependent differential in the fishing mortality rate was maintained during the 1970s, when only a sport fishery was active (Baker et al. 1976; Duckworth and Paine 1975).

In most cases the behavior of the model under schedule C (Fig. 5–9) is similar to that exhibited by the real population. In particular, the observed increase in recruitment after 1968 is predicted reasonably well, as is the increase in overall abundance — the predicted 1975 abundance levels corresponding roughly to Nepszy's (1977) evaluation of the current status of the population. Only the simulated lengths at various ages (Fig. 9) differ consistently from those observed. It is noteworthy that if the observed values for length at age 4 are imposed on the model rather than the values generated by equation 2, the simulated commercial catch follows a pattern almost identical to that observed (Fig. 5).

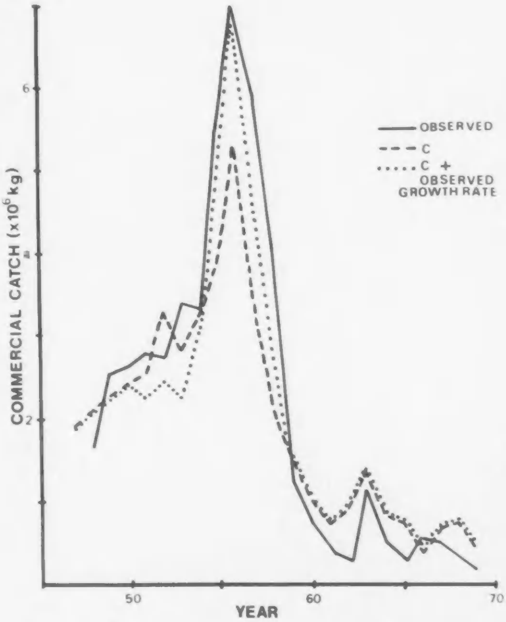

FIG. 5. A comparison of the observed commercial fisheries catches with catches predicted by the model using survival rate schedule *C* alone and survival rate schedule *C* + observed growth rate.

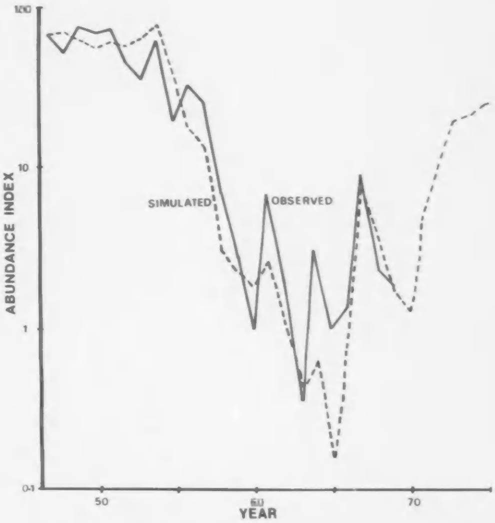

FIG. 6. A comparison of the observed abundance indices (number fish per trap net lift) for fish age 2 and over with values generated by the model using survival rate schedule *C*.

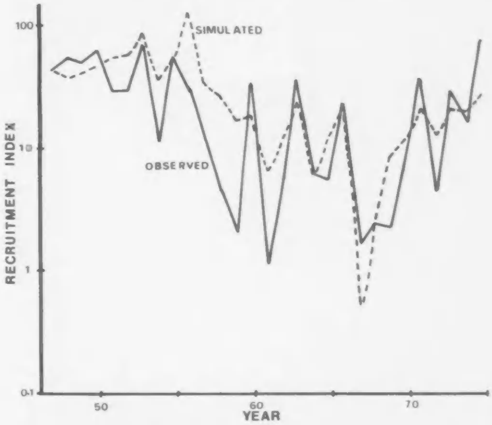

FIG. 7. A comparison of the observed values for the recruitment index (number 1 yr olds per trap-net lift) with values generated by the model using survival rate schedule *C*.

Evaluation of Analyses and Simulation

We have shown that the available information on relative abundance, year-class strength and growth for western Lake Erie walleye can be used to construct a quantitative version of the qualitative model outlined in the introduction. In addition, we have shown that a reasonable representation of the actual fishing mortality regime during 1947–75 will elicit from this model an overall pattern of behavior very similar to that exhibited by the real population. It is particularly note-

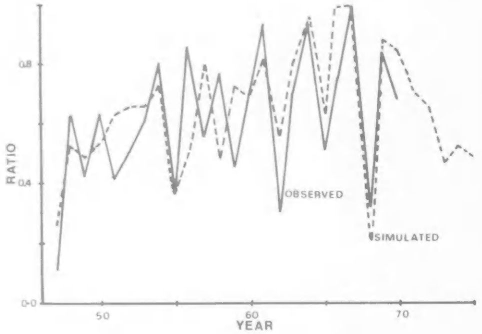

FIG. 8. A comparison of observed values for the ratio of 2-yr-old abundance to the abundance of fish age 2 and over with values generated by the model using survival rate schedule *C*.

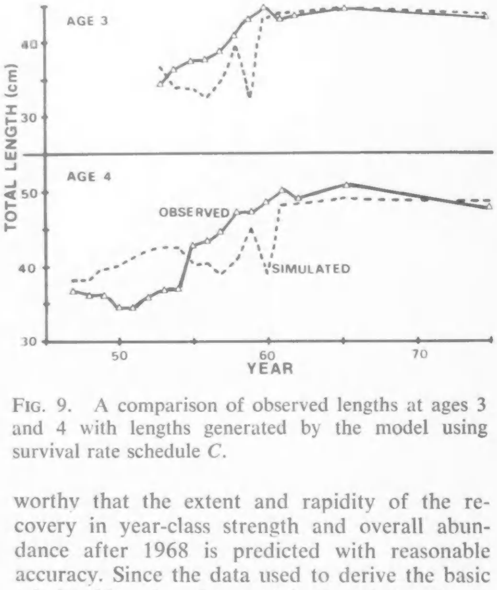

FIG. 9. A comparison of observed lengths at ages 3 and 4 with lengths generated by the model using survival rate schedule *C*.

worthy that the extent and rapidity of the recovery in year-class strength and overall abundance after 1968 is predicted with reasonable accuracy. Since the data used to derive the basic relationships for the model extended only to 1968, this suggests that quantitatively similar relationships were still operative in the population after this date and that the model has true predictive capabilities.

The ability of the model to reproduce historical changes in relative abundance does not stem solely from the fact that data on these same changes were used in deriving the model. The fit to historical data was obtained by comparing observed and simulated commercial catch values. To generate these values, independent information on the following factors had to be incorporated into the model: natural mortality, the relation between absolute population size and the relative abundance index used, and the relation between length and weight. It does not follow that such a model would necessarily be capable of generating reasonable commercial catch values for 1947–69 simply because it was derived in part from estimates of relative abundance and lengths at various ages for this same period. Similarly, even if reasonable catch values could be generated under a realistic fishing mortality regime, it does not follow that the corresponding behavior of other population indices would necessarily mimic their observed behavior. The fact that the model does behave in this manner suggests that the various measures of abundance, year-class strength, and growth used in deriving it were reasonably consistent and representative. It also suggests that given the levels of recruitment observed, the loss to the fishery over this time period was sufficient to account for the observed decline in overall abundance.

Analysis of Alternative Harvest Strategies

In this section we attempt to derive an optimal harvest strategy for the population, allowing for the known effects of climatic variation on recruitment. The sensitivity of such a strategy to changes in growth rate, gear selectivity, and natural mortality is also evaluated.

Cohort yield model — Much theoretical work has focused on determining the maximum yield obtainable from a single cohort of a multi-age fish stock. Beverton and Holt (1957) showed that yield curves peak at low fishing mortality rates when the natural mortality rate is low. At high natural mortality rates, these peaks disappear and maximum yields are then obtained at the highest fishing mortality rates. Thus, a strategy to maximize yield from a cohort will be sensitive to estimates of natural mortality.

We used the following model to assess the effects of variations in natural mortality and catchability on maximum cohort yield:

$$N_{i+1} = N_i e^{-(F_i + M_i)}, \quad i = 1\text{–}10$$

$$F_i = fq_i$$

$$Y = \sum_{i=1}^{10} W_i \frac{F_i}{F_i + M_i} (N_i - N_{i+1})$$

where N_i is the number of fish aged i at the start of the year, F_i and M_i are the instantaneous rates of fishing and natural mortality for age i fish, f is the fishing effort, q_i is the catchability of age i fish, Y is the total yield from the cohort, and W_i

TABLE 3. Maximum annual yields and optimal fishing efforts for a single cohort and for a population under various entry and natural mortality regimes. Catchability values for ages 1 through 3 are defined as follows — I: 0.17, 0.47, 0.83; II: 0.05, 0.50, 1.0; III: 0.0, 0.02, 0.42. A value of 1.0 is assigned to fish age 4 and over. Natural mortality coefficients are the same for all age-classes.

		Cohort[a]		Population	
Entry regime	Natural mortality coefficient	Optimal effort (yr^{-1})	Maximum yield (10^6 kg/yr)	Optimal effort (yr^{-1})	Maximum yield (10^6 kg/yr)
I	0.2	0.4	2.1	0.2	5.3
III	0.2	0.7	2.5	0.3	6.8
II	0.2	0.4	2.1	0.2	5.4
II	0.3	0.6	1.6	0.2	2.6
II	0.4	1.0	1.3	0.5	1.5

[a] Initial density: 5×10^6 1 yr olds, each with a total length of 15.2 cm.

is the weight of age *i* fish halfway through the growing season. Values for W_i were calculated from equations 3 and 4 assuming a length at age 1 of 15.2 cm. A value of 5×10^6 fish was assumed for N_1.

The optimal fishing effort generated by this model varied for different age-dependent catchability regimes and for different natural mortality rates. To illustrate the first effect, two extreme catchability regimes reflecting early and late entry to the fishery (regimes I and III in Table 3) were used. The late-entry regime approximates the real situation for western Lake Erie walleye in 1948, and the early regime the real situation in 1963. In both, the catchability coefficients for fish age 4 and over were set equal to 1.0, reflecting full recruitment to the fishery. A third catchability regime (II in Table 3), intermediate between the extremes of I and III, was used to illustrate the effects of variations in the natural mortality rate on the optimal fishing effort.

A comparison of the results (Table 3, Fig. 10) revealed higher optimal efforts and yields for the delayed-entry regime than for the early-entry regime. Furthermore, increasing effort beyond the optimum did not decrease yield as rapidly in the delayed-entry situation as it did in the early-entry situation. Increasing the natural mortality rate led to an increase in the optimal effort and a decrease in the yield produced by that effort.

Stochastic population yield model — An analysis of the maximum yield derivable from individual cohorts is of limited use in determining strategies to maximize sustainable yield. An equally important factor to consider is future recruitment through natural reproduction. Using the stock–recruitment relationship derived for this population, we extended the previous analysis of yield to include the effects of breeding stock size and climatic variation. The model for this analysis is functionally identical to that used to describe the historical behavior of the population. However, instead of using observed rates of spring warming, we simulate the catch for a 100-yr period using a sequence of warming rates drawn at random from the empirically determined probability distribution for that quantity.

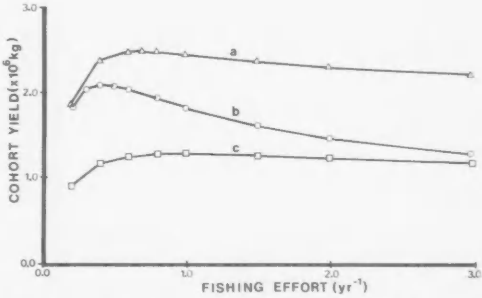

FIG. 10. Yield versus effort curves for a single cohort. The three curves represent different natural mortality rates (M_i) or entry regimes (see Table 3): (a) entry regime III, $M_i = 0.2$; (b) entry regime I, $M_i = 0.2$; (c) entry regime II, $M_i = 0.4$. Initial conditions: 5×10^6 yearlings with a length of 15.2 cm.

The effects on optimal effort of variations in natural mortality and catchability were not as strong in these population simulations as they were in the cohort simulations (Table 3). However, the effects on the maximum yield were somewhat stronger. In addition, the yield curves for the population were more sharply peaked than those for the cohort (Fig. 11). Delayed entry to the fishery again produced a higher yield, which showed less response to increasing effort. However, the predictions of high yields at low efforts may be suspect.

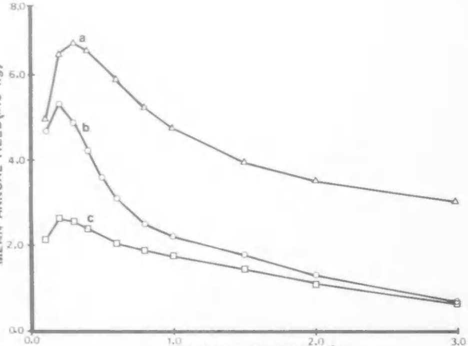

FIG. 11. Mean annual yields from a walleye population subjected to constant fishing effort for a 100-yr period. The three curves reflect different natural mortality rates (M_i) or entry regimes (see Table 3): (a) entry regime III, $M_i = 0.2$; (b) entry regime I, $M_i = 0.2$; (c) entry regime II, $M_i = 0.3$.

A major deficiency in the population model is the assumed constancy of the natural mortality rate. At low fishing mortalities, the relatively low estimate for natural mortality (20%) causes the total instantaneous mortality rate to be low. Under these conditions, the population density increases to very high levels. This occurs because the slope of the stock–recruitment relationship decreases asymptotically to zero with increasing stock size and therefore does not act to stabilize population density. Although our analysis of the data on breeding stock size and recruitment did not reveal a dome-shaped stock–recruitment curve, general considerations as well as evidence from other populations (e.g. Forney 1976) suggest that some form of density-dependent regulation should occur. At the present time, however, we do not know whether this regulation will be reflected in the natural mortality rates of yearling and older fish or in the mortality of eggs, larvae, and juveniles. Without this information, we cannot place much confidence in the high mean annual yields predicted for relatively low levels of fishing effort. A greater degree of reliability can be attached to the general pattern of response exhibited by the optimal fishing effort to the kinds of changes in the character of the fishery explored in these simulation studies.

Stochastic dynamic programming analysis — Another approach for estimating the maximum sustainable yield of walleye in western Lake Erie is to determine the balance between yield and future recruitment from the cohort. A technique to evaluate optimal fishing effort in this way can be derived from the principles of stochastic dynamic programming (Walters 1975). This technique allows the development of management strategies based on standing stock, or some other measure of population density, and a particular management objective (e.g. maximum sustainable yield or minimum variation in catch). The dynamic programming approach applied to fisheries by Walters (1975) was designed for populations with nonoverlapping generations. Since walleye do not conform to this assumption, we used a modified version of Walters' approach.

Instead of focusing on the total stock, we determined the optimal effort for exploiting a cohort throughout the time it is resident in the population. This was done by assigning to each cohort, of a given size at age 1, a numerical value equal to the total yield derived from that cohort plus the mean annual value of the offspring of that cohort. The degree of fishing effort which maximized this value was defined as the optimal effort. The value of the offspring was determined from their number by a recursion process described by Walters (1975). The number of offspring was a function of the number of reproducing adults in the cohort and the rate of spring warming. A stochastic element was introduced into this scheme by defining the spring warming rate in terms of its empirically determined probability distribution. The model which forms an essential part of this analysis was based on the cohort yield model described above and the stock–recruitment relationship. Young-of-the-year (YOY) index catch values were used as indicators of numerical abundance at age 1. Recruitment to the fishery was defined by the moderate entry regime described earlier (regime II, Table 3). A constant annual natural mortality rate was assumed for all age-groups.

This approach yielded an optimal control law for the fishery defined in terms of the optimum harvest appropriate to a year-class whose strength was characterized by a particular YOY value (Fig. 12). The range of fishing effort required to implement this law over the range of YOY values considered was given in terms of a frequency distribution (Fig. 13).

Our analysis of the growth rates of individual walleye revealed a density dependent effect. Although this regulation of growth is included explicitly in the long-term population model described earlier, its effects could only be explored indirectly using the dynamic programming approach. This was done by carrying out separate analyses assuming that (1) the YOY index value represents recruitment to a population with low overall density, thus allowing a high rate of growth for recruits (L_1 = 28 cm.); and (2) the

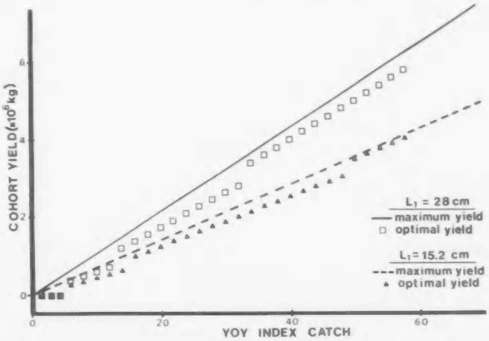

FIG. 12. The relationship between optimal cohort yield and cohort strength, generated by the dynamic programming technique, for two different growth rates (L_1 = 15.2 cm and L_1 = 28 cm.). The corresponding relationships between maximum cohort yield and cohort strength are also included.

YOY index represents recruitment to a dense population, thus imposing a low growth rate on recruits (L_1 = 15.2 cm.). The instantaneous natural mortality rate was held constant at 0.2. As expected, a higher growth rate resulted in higher yields (Fig. 12) and slightly higher effort (Fig. 13a, b). In both cases, the optimal cohort yields calculated by this approach were not much lower than the maximum yields obtainable when no value was attached to future recruitment (Fig. 12). Despite the differences in yield due to differences in growth rate, predictions of optimal effort were similar to those generated by the long-term population model. The optimal control laws in Fig. 12 indicate an optimal fishing effort of 0.2 per yr with highest frequency (Fig. 13a). This prediction corresponds well to the prediction of the population model (Table 3). Furthermore, increasing the natural mortality rate to 0.4 per yr leads to an optimal effort prediction of 0.5–0.6 (Fig. 13c), which again corresponds to the predictions of the population model (Table 3).

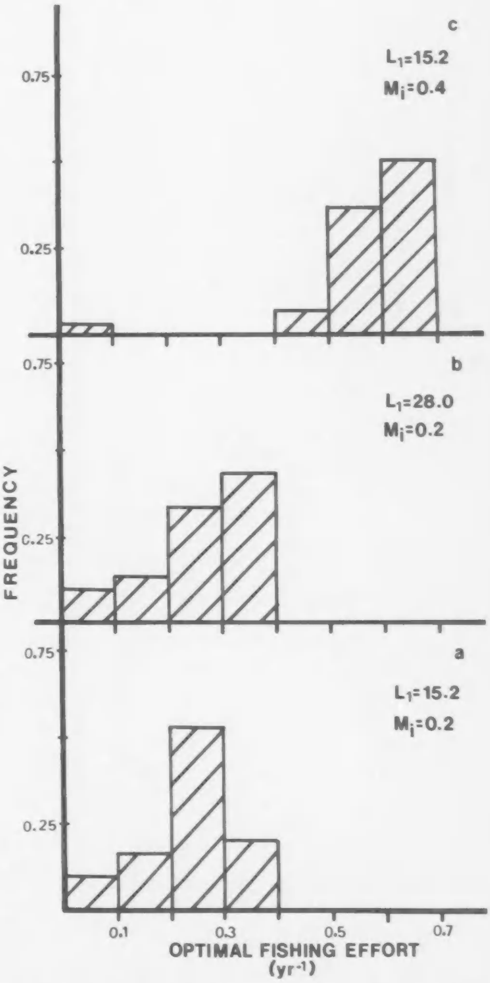

FIG. 13. Frequency histograms for the optimal fishing efforts associated with the optimal cohort yields given in Fig. 12 (a and b) and for a condition of increased natural mortality (c).

Evaluation of Optimal Harvest Strategies

The similar predictions of optimal effort generated by the two models that consider yield and future recruitment suggest that a more efficient management policy could be developed for the exploitation of western Lake Erie walleye. However, the magnitude of the resulting catches is currently beyond our predictive capability. The optimal catches generated by these models probably overestimate the optimal catches actually obtainable. This is due in part to our inability to define the effects of high population densities on the mortality rates operative at various life stages. For the same reason, it is not certain that the actual yield vs. effort curve would exhibit the sharp peak at low fishing efforts that was characteristic of the curves generated by our models. A broad dome in this curve would allow a fairly wide range of fishing effort without major differences in yield.

Nevertheless, both models indicate optimal instantaneous fishing mortality rates of 0.2 to 0.3 per yr, assuming a value of 0.2 for the natural mortality rate. Even at higher natural mortality rates, the optimal fishing mortality rate does not increase beyond 0.6 per yr. These figures are in sharp contrast to those obtained from the estimated survival rates in Fig. 1. Assuming a natural mortality rate of 0.2, the fishing mortality rates for fully recruited age-groups range from 0.7 in 1948 to 2.8 in the mid-1960s. These figures indicate that this population has long been exploited at levels beyond the optimum.

The simulation results also demonstrate that a catchability regime that emphasizes delayed entry into the fishery yields greater harvests, which are less sensitive to supra-optimal exploitation than a regime that allows early entry.

Conclusions

Analysis of the data made available to us suggests that greatly increased exploitation of western Lake Erie walleye during the 1950s and 60s reduced overall population abundance to very low levels over a relatively short time. Data collected during this period appear to contain extractable information on the relations linking year-class strength to breeding-stock size and the spring water temperature regime, as well as on the relation linking growth rate to population density. A model based on preliminary estimates of these relations was relatively successful in accounting for the known behavior of the population and was readily adaptable for use as a management tool. It may be possible to extend and refine this model to the point where it could be used in developing realistic management policies for the population.

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Responses of Percids to Exploitation[1,2]

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Conventional exploitation is described as an opportunistic process directed initially toward the largest members of the fish community and preferentially selecting those species for as long as the fishery persists. Some responses of percid communities to exploitation stress are similar to those previously described for marine stocks and salmonid communities. The most conspicuous responses of percids are changes in variability of recruitment, increases in growth rate, and reductions in the ages of first spawning. The least tractable and potentially most malefic responses are changes in genetic stocks and in interspecific relationships within the aquatic community. Three models are proposed for early detection of exploitation stress in fish stocks or communities.

Key words: Percidae, exploitation, community ecology

SPANGLER, G. R., N. R. PAYNE, J. E. THORPE, J. M. BYRNE, H. A. REGIER, AND W. J. CHRISTIE. 1977. Responses of percids to exploitation. J. Fish. Res. Board Can. 34: 1983–1988.

Les auteurs décrivent l'exploitation convientionnelle comme étant un processus opportuniste dirigé au début vers les plus grands membres de la communauté de poissons et recherchant ces espèces de préférence aux autres aussi longtemps que dure la pêcherie. Certaines réponses des communautés de percidés aux contraintes de l'exploitation sont semblables à celles déjà décrites pour les stocks marins et les communautés de salmonidés. Les réponses les plus évidentes des percidés sont des changements dans la variabilité du recrutement, des diminutions du rythme de croissance et un abaissement des âges de la première fraie. Les réponses les plus difficiles à déceler et possiblement les plus dommageables sont des changements dans les stocks génétiques et dans les relations interspécifiques au sein de la communauté aquatique. Les auteurs proposent trois modèles visant à détecter dès le début le stress dû à l'exploitation dans des stocks ou des communautés de poissons.

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To identify generalized responses of percid populations and communities to stresses imposed by exploitation we would prefer data from lakes where only that one stress has operated recently. Unfortunately most lakes for which data are available have been subjected to a multiplicity of cultural stresses, including especially eutrophication, introduction or invasion of exotic species, and overt alteration of habitat through pollution or shoreline modification. Nevertheless, we may be able to infer the directions of certain responses even though we are unlikely to achieve precision or clear discrimination of responses to this stress compared to some others.

We characterize conventional exploitation as an opportunistic process directed initially toward the larger members of the fish community and subsequently toward smaller fishes as the larger species decline in abundance. This sequence has been identified in connection with the successive decline or collapse of many of the salmonid fisheries of the world (Regier and Loftus 1972). Its application to percids stems in the first instance from the observation that some of our percid communities exist by default of the salmonid communities that preceded them (Regier and Loftus 1972; Colby et al. 1972).

As exploitation proceeds, it is important that the perceived relative value of the species initially sought does not change greatly. Thus, a large piscivore such as a lake trout or pikeperch will be much esteemed by fishermen long after it has ceased to be a conspicuous component of the yield. Under conditions of a sustained demand we can expect an opportunistic fishery to persist in taking the premium species whenever they are available.

North American and European fisheries seem to have followed similar sequences of development, initially exploiting the native fish communities in culturally unstressed waters (i.e. unstressed by those conditions historically accompanying human population growth) and proceeding from this frontier through a number of stanzas which include overexploitation of the premium species and simultaneous intensification of effort directed at secondary species (Regier 1976). Repetition of this sequence generally results in a shift in the species composition of the community such that the largest (generally benthic and/or piscivorous) species are reduced in abundance, while smaller (generally pelagic and/or planktivorous) species become more prominent. This process is characteristic of unlimited-access fisheries irrespective of whether the motivation for fishing is recreational or commercial. The only tangible difference between these fisheries lies in the efficiency with which the fishing gear captures fish.

Among the set of percid communities discussed at this symposium, we have identified five general responses to exploitation. Three of these, i.e. changes in variability of recruitment, changes in growth rate, and alteration of the age at first spawning, are manifestations of any selective force of mortality operating upon the exploited population. These were identified in some of the major oceanic fisheries even before the turn of the century (Cushing 1972) and have recently been detailed for salmonid communities in oligotrophic lakes (Regier and Loftus 1972). The two remaining responses are far more subtle, but in our view, more likely to result in irreversible changes in percid communities. These responses are changes in the genetic compositions of wild stocks and biological interactions between percids and other species in the community. Following a brief description of some percid examples of responses to exploitation, we offer a framework for detection of the more subtle responses.

Changes in Variability of Recruitment

In the Minnesota waters of Lake of the Woods, variation in walleye, *Stizostedion vitreum vitreum*, recruitment increased from 1947 to 1973 as indicated by catch-per-unit-of-effort (CPUE) data (Schupp and Macins 1977). Forney (personal communication) cautions against a reliance on CPUE in recreational fisheries as an indicator of abundance, since the yield of a fishery that depends upon a feeding response in the species sought (i.e. baited hook) is related to the status of the entire fish community rather than being solely a function of abundance of the target species. In Lake of the Woods the commercial fishery has been reduced since 1959 but growth in recreational fishing has kept effort at a high level. In recent years the combined yield from the two fisheries was similar to the total commercial harvest (approximately 2.2 kg/ha) in 1935.

In Lake Erie, walleye and yellow perch, *Perca flavescens*, have oscillated in abundance during the intensive fishery of the past 25 yr (Nepszy 1977). Walleye stocks in western Lake Erie collapsed in the 1960s following a many-fold increase in fishing effort. Abundance has subsequently increased by virtue of the strong year-classes of 1970, 1972, and 1974. These walleye have been subjected to lower exploitation levels because of mercury contamination which has made the larger fish unmarketable (Shuter and Koonce 1977). Yellow perch stocks in Lake Erie also underwent a decline in the early 1970s. Recent indices of abundance (CPUE in experimental trawls) indicate relatively weak year-classes over a broader span of years than was previously common.

Overall, recruitment for these perch stocks has become more variable in both amplitude and frequency.

Changes in Rates of Growth and Maturity

Increased growth rates in exploited populations are commonplace and require no elaboration here. However, growth rate may be one of the most sensitive characteristics to examine in attempting to quantify the effects of exploitation. While growth rates are among the most labile of biological characteristics, occasionally compromising their utility in drawing comparisons between populations, they are among the most responsive to temperature (Kitchell et al. 1977). This allows considerable precision in accounting for the influence of a major abiotic variable.

Growth data are available for many populations of percids that have collapsed in the presence of intensive fisheries. Growth rates of these stocks may well represent maxima for the species under prevailing temperature conditions. Certainly, it is no mere coincidence that very rapid growth rates are frequently observed in stocks undergoing severe declines in abundance. For example, the growth rates of female walleye in Lake Erie during 1927–33 (18 cm at age 2; Deason 1933) were considerably slower than during 1964–66 (37 cm at age 2; Parsons 1972). The latter period was immediately preceded by a many-fold decline in abundance of the western Lake Erie stocks (Regier et al. 1969).

For teleosts in general, age at first maturity decreases as growth rate increases, although the converse is true in some stunted populations (Alm 1959). Percid examples of a reduction in age at maturity are available from Lake Erie, where Wolfert (1969) compared maturation of walleye in 1964–66 with data for 1927–28 (Deason 1933). In their earlier period, female walleye matured at ages 4 and 5, whereas males matured at 3 and 4. During the later period, and concomitant with an accelerated growth rate, 85% of the females were mature at age 3 and 99% were mature by age 4. Over 95% of the male walleye matured by age 2 during the later study period.

Yellow perch in the western basin of Lake Erie showed a similar change in the maturation schedule. Average age for the majority of females spawning for the first time shifted from age 3 during 1927–37 (Jobes 1952) to age 2 during 1960–66 (Nepszy personal communication).

Changes in Genetic Stocks and Community Interactions

Until recently, insufficient consideration has been given to the need for identification, monitoring, and protection of genetic stocks (Ricker 1972; Loftus 1976). Many river- and bay-spawning stocks of percids have been exterminated by cultural sources of stress, including exploitation (Schneider and Leach 1977). Loss of these stocks may have gone unnoticed in the past during the typical "fishing-up" process (Regier and Loftus 1972; Smiley 1882) or wherever catch statistics were compiled over areas broad enough to preclude observation of the sequential collapse of individual stocks (Lawrie and Rahrer 1972; see also Cushing 1976, p. 280, for a quote by C. G. J. Petersen (1894) on the dangers of "fishing-up").

Populations of *Stizostedion* sp. in large lakes are characterized by discrete stocks which "home" to their own spawning grounds. The resulting heterogeneity in time and place of spawning serves as a buffer against certain highly variable environmental circumstances. The Bay of Quinte walleye population, for example, probably survived because remnants of river-spawning stocks were reproductively successful after all lake spawning had failed. It is, of course, fortuitous that persistence of the Bay of Quinte walleye was augmented by the tenacity of river-spawning stocks. The reverse condition (i.e. river-spawning stocks predeceasing spatially associated lacustrine stocks) has generally been the case for walleye (Schneider and Leach 1977; Spangler et al. 1977) and lake whitefish, *Coregonus clupeaformis* (Smiley 1882) in the Laurentian Great Lakes, since fluvial environments were the earliest to be degraded by agricultural and industrial "development."

If the existence of discrete spawning stocks enhances the likelihood of perpetuation of the population, then fishing effort and catch levels appropriate to an entire population may have disastrous consequences when confined to a single stock or subpopulation. This has been recognized for salmonid stocks whose ranges are geographically separate (Lawrie and Rahrer 1972), but it logically applies also to stocks that are isolated from each other only at spawning time.

Much of the problem of identifying exploitation effects on the genetic composition of a population lies in evaluating the genetic contribution to an observed response. Again, growth rate exemplifies the problem, since the literature includes many reports of fast- and slow-growing groups of perch within the same water body (e.g. Krasikova 1958; Svetovidova 1960; Nikolsky 1965; Balon 1967). The mechanisms responsible for this segregation of growth groups have not been identified with certainty, but imply genetic or behavioral differences (perhaps genetically based) within these populations. These differences become apparent in migratory behavior, spawning site and time (Chikhova 1973), habitat preference (Schneider 1908), food preference, and feeding behavior (Il'ina 1973).

A priori it is to be expected that individuals will vary in these characteristics, but it is not clear to what extent the populations are differentiated into discrete stocks maintained as such by genetic differences. Chikhova (1973) reported morphological distinctions between the subpopulations spawning in different regions of the Kuybyshev Reservoir, but Il'ina (1973) showed that in an experimental pond population, progeny from one source segregated into three ecological groups (planktophages, benthophages, and cannibals) within a few weeks after first feeding. Such observations suggest existence of separate stocks, but we found no definitive proof that the distinctive features of these subpopulations are heritable.

It has been shown experimentally (Simpson and Thorpe 1976; Thorpe 1977) that some growth characteristics of Atlantic salmon, *Salmo salar*, depend upon genetic factors and the possibility exists that similar controls occur among percids. Of greatest concern is the possibility that a strongly size-selective fishery might endanger or annihilate a stock genetically predisposed to rapid growth. Such a change in the population may well go unnoticed during a "fishing-up" process.

Stress-Response Models

We turn now to consideration of three processes that may be operative in producing the symptoms of stress from exploitation discussed above. Assume (a) a reasonably complex ecosystem in which some of the larger percid species are represented by more than one stock; (b) that the stocks initially exhibit an appreciable degree of reproductive isolation; (c) that taxonomic methods can distinguish between the stocks before the onset of fishing; and (d) that "fishing-up" occurs as a result of the conventional exploitation process defined above. Under these conditions, we may expect the following events to occur at some point(s) during the "fishing-up" sequence:

(i) Interstock desegregation. Different stocks of the same species, at least those whose geographic ranges overlapped initially, will desegregate or introgress with a consequent reduction in the number of stocks. Perhaps, eventually, only one stock will be the result. Detection of this process may be accomplished through monitoring a full range of taxonomic features and analyzing these with appropriate statistical techniques. The emergence of individual intergrades or a spreading and fusion of clusters to produce a single undifferentiated group of points will confirm the presence of the desegregation process.

(ii) Interspecific desegregation. Perhaps even before all the stocks of a particular species have desegregated genetically to form a single gene pool, some behavioral and genetic desegregation may occur between closely related species (Regier 1968). The likelihood may be high that such hybrids will be poorly programmed for effective spawning and/or be physiologically sterile. Introgression of this kind, leading to parthenogenetic reproduction, may have been responsible for the great preponderance of female chubs (*Coregonus hoyi*) reported for Lake Michigan (Brown 1970). This seems plausible in view of the apparent parthenogenetic reproduction of goldfish, *Carassius auratus*, following an inefficient fertilization by males of closely related species (Leider 1955, cited by Alm 1959). In any event, taxonomic analyses should serve to identify instances of interspecific desegregation when it occurs and to document any continuing trend to greater desegregation as exploitation intensifies. By monitoring space–time trajectories of individual cohorts, it may also be possible to document decreasing precision of "homing" for purposes of spawning.

(iii) Proliferation of life-history stanzas. As "fishing-up" proceeds, larger species are reduced to low levels of abundance and the less preferred, smaller species may have an opportunity to add another "life-history stanza" at the end of their usual maturation sequence. This may involve a shift of the larger individuals to a diet of larger food particles which may trigger a renewed burst of growth. Ecologically, such individuals take on, in part, a role that was earlier maintained by some of the larger species or stocks now suppressed by the fishery. Detection of this process, if and when it occurs, should be possible through monitoring age and growth data for succeeding cohorts.

The kinds of data that would be useful and perhaps sufficient for purposes of objective, detailed tests have been specified above for each of these models. It is unlikely that such precise data are commonly available, but less detailed data of other kinds do exist that have some bearing on these questions. For example, the fish communities of numerous lakes were described a century or more ago by perceptive and well-trained naturalists, systematists, and fishery overseers. Comparison of these accounts with more recent data in light of the above hypotheses may serve to alter our confidence in the validity of the postulated cause–effect relationship.

Models of the type discussed above offer some hope that we may eventually be able to detect exploitation effects before some critical point has passed in the continual restructuring of the fish community. This approach is essentially "equilibrium-centred", i.e. more concerned with rationalizing fluctuations in abundance of specific stocks than with identifying relationships that enable the entire fish community to persist in spite of exogenous perturbations. We need also to develop models that are useful in determining what Holling (1973, 1976) describes as the "resilience" of the fish community, indeed, of the aquatic ecosystem. With these tools in hand we might profitably question why intensively exploited fish stocks do not always rebound following a recession of exploitation (e.g. Windermere perch, Le Cren et al. 1972). We may also understand how exploitation pre-conditions fish communities for collapse in the face of other unanticipated (though inevitable) changes in the ecosystem.

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Structure and Transformation of Fish Production Systems[1,2]

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KERR, S. R. 1977. Structure and transformation of fish production systems. J. Fish. Res. Board Can. 34: 1989–1993.

A tentative synthesis is provided of some considerations that emerged from the PERCIS proceedings. The percid composition of commercial fisheries tends to be relatively conservative except where abrupt community transformations, characterizable as fold catastrophes, mark the effects of critical conjunctions of fishing intensity and lake productivity acting jointly as control variables. These behaviors of fish production systems are consistent in general with current observations and theory based upon size-dependent processes in marine pelagic fisheries.

Key words: theory, percidae, community ecology, fishing intensity, production systems

KERR, S. R. 1977. Structure and transformation of fish production systems. J. Fish. Res. Board Can. 34: 1989–1993.

L'auteur fait une synthèse préliminaire de certaines considérations émergeant des comptes rendus de PERCIS. La composition en percidés des pêches commerciales tend à être relativement conservatrice, sauf dans les cas où d'abruptes transformations dans les communautés, qu'on peut caractériser comme catastrophiques, résultent de conjonctions critiques de l'intensité de la pêche et de la productivité des lacs, agissant conjointement comme variables de contrôle. Ce comportement des systèmes de production de poisson est en général conforme aux observations et à la théorie courantes fondées sur des processus associés à la taille dans des pêcheries pélagiques marines.

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IN this paper, I attempt nothing more than a limited, highly personal, and tentative exploration of certain considerations raised during the PERCIS proceedings. Various insights and information were presented during the symposium but it is too soon, by at least several years, to attempt a general synthesis of the major results. Conceptual developments mature slowly with time and perspective, a process that cannot be hurried. In time, perhaps, the views herein may even prove to be correct and useful. For now, however, they should be viewed as suggesting some possible forms for future synthesis.

Percid Community Composition

The question of community discreteness usually leads to spirited discussion. Some workers consider that characteristic assemblages of species are commonplace and represent recognizably discrete communities; others, impressed by the great variation and apparent intergradation of natural assemblages, suggest that observed communities are mere typological reflections of environmental gradients and lack innate reality.

Appreciable effort was directed, at various times during the symposium, toward devising some unequivocal definition of a "percid community." Not unexpectedly, these efforts inevitably foundered upon the ubiquitous exceptions that plague attempts at ecological classification. The usual, if unsatisfactory, conclusion was that a percid community is best defined as any aggregation of percids in a body of water.

Nevertheless, the impression to be gained, in particular from the symposium participants who have had substantial field experience of percids, is that there is something more to the problem: that there are in fact recognizable associations of species that, in experiential terms at least, qualify unarguably as percid communities. The difficulty, as always, is to abstract and quantify the relevant criteria in a form that is consistent and meaningful to those of us who lack the requisite field experience.

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[1] This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2] Bedford Institute of Oceanography Contribution.

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In this context, the paper provided by Adams and Olver (1977) is especially useful. One of the conclusions they offer is the tentative generality that percid species tend to constitute about 30%, by weight, of the fish yield obtained from communities in which they occur. If such a system conservatism is real, in the sense that a "30% rule" constitutes a reliable measure of central tendency for communities containing percids, then a phenomenon of considerable interest has been observed. The implication is that a "30% rule," or any similar structural conservatism, should reflect underlying organizational properties that could lead to an operational understanding of fish communities.

The proportional representation of percids, mostly walleye, in the average fish yields of the 70 lakes described by Adams and Olver is depicted in Fig. 1. The observed distribution is skewed, and possibly bimodal, with modes occurring on either side of the putative 30% norm. The appearance of bimodality occurs because only two lakes fall within the range of 26–29% percids. In view of the heterogenous lake types assembled by Adams and Olver, some stratification of the sample seems in order. In Fig. 2 I have restricted the data set to include only lakes between 1000 and 6000 ha of surface area. The effect of lake surface area on a fishery and its yield has been discussed by Ryder et al. (1974); it is enough for present purposes to note that a surface-area effect for percids would be especially consistent with the lotic-environment hypothesis generated for percids by Kitchell et al. (1977). The lake size-intervals chosen for Fig. 2 are arbitrary, except that a bare majority of the 70 available lakes could thereby be retained for analysis, within a relatively narrow range of lake sizes. It is sufficient to note that imposition of similar criteria for area stratification do not appreciably modify the resulting distribution.

A further inhomogeneity in the remaining data set (Fig. 2) is caused by seven lakes with high morphoedaphic indices (MEI > 10) and, hence, high potentials for fish production (Ryder et al. 1974). Deletion of these lakes from the sample leads to a distribution that is somewhat nearer normal, but the suggestion of biomodality near 30% percids has not been removed. The effects of both sample stratifications have been to remove a tendency for large lakes and unusually productive small lakes to provide relatively smaller percentages of percids to their fisheries. Unfortunately, the sample size has been so reduced by stratification that firm conclusions are inadvisable. But perhaps it is reasonable to say that large or productive lakes tend to produce about 20% percids, and smaller, unproductive lakes about 35% percids on the grounds that the sample stratifications have shifted the mode from the first value to the second. In effect, there is no reason to reject the community conservatism suggested by Adams and Olver, although the details seem rather complicated.

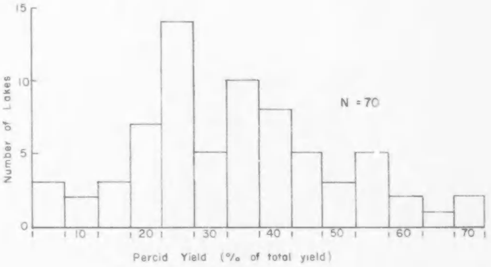

FIG. 1. Percentages of percids by weight, in the average yields from 70 northern Ontario lakes. Indicated percentage is the highest value for the interval. (Data from Adams and Olver 1977.)

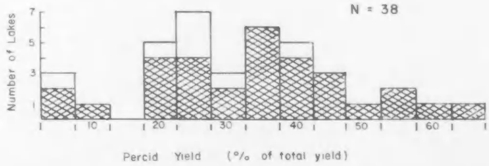

FIG. 2. Subset of the lakes from Fig. 1 for surface areas between 1000 and 6000 ha. See caption to Fig. 1. Open parts of bars indicate lakes with morphoedaphic indices >10.

Community Transformations

Considering again the stratified sample of 38 small lakes (1000–6000 ha), there is a tendency for percid contribution to the average catch to decline as either fishing effort (measured as relative yield intensity, RYI, by Adams and Olver) or lake productivity (MEI) increases. The joint effect of these factors is shown in Fig. 3. Proceeding from the origin, the diagonal construction line A passes first through a zone of high percid percentages, next a mixed zone of both high and low percentages, and finally an outer zone of low percid percentages.

The tendency for percid representation to decrease at high levels of either RYI or MEI is noteworthy, but the separation into three zones in Fig. 3 is particularly so, because of its possible implications for community structuring. Considered as a topological surface, the central zone of mixed percentages appears to represent a fold.

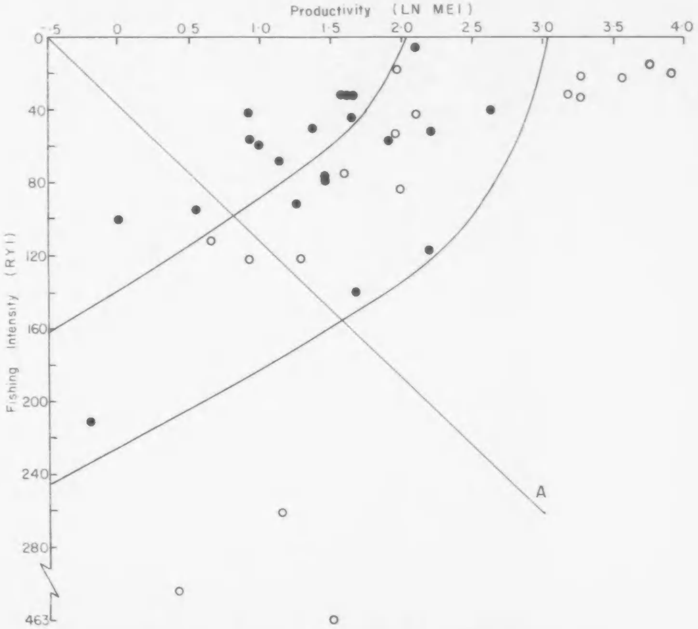

FIG. 3. Relation of fishing intensity (RYI) to lake productivity (MEI) for a sample of northern Ontario lakes between 1000- and 6000-ha surface area. Open circles represent <30% percids, closed circles ≥30% percids.

That is, proceeding from the origin along A, there is an upper surface reaching to the margin of the outer zone, which then folds under itself, back to the margin of the inner zone, and finally emerges as the lower surface. In cross section along A, this structure is depicted schematically in Fig. 4.

By this reasoning, Fig. 3 depicts a fold catastrophe (Thom 1975; Zeeman 1976), where MEI and RYI are the two required control variables and percid percentage is the resulting system behavior. In mathematical terms, the upper and lower surfaces are attractors for community behavior, and the connecting middle sheet, the separatrix, is a surface of low probability; hence the apparent bimodalities of Fig. 1 and 2.

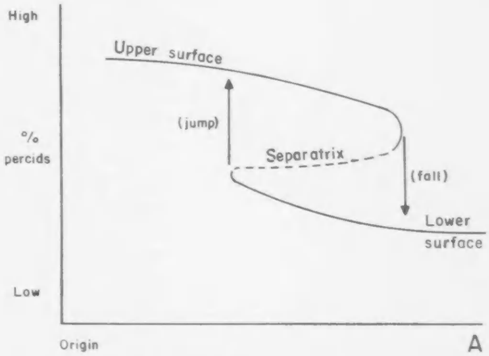

FIG. 4. Schematic section along the construction line A of Fig. 3.

If we accept that an ensemble of lakes, such as the data depicted in Fig. 3, is equatable in a sense (Ryder et al. 1974) with the time series behavior of a single lake being manipulated by changes in the two control variables, a picture of discrete community structures, with abrupt transformations between them, then emerges. Thus, if we start with a hypothetical unfished lake of low MEI and steadily increase the fishing intensity, RYI, the percentage of percids will remain high until the edge of the fold on the upper surface is reached. At this stage, the fishery will abruptly change to a low percentage of percids, as the system behavior falls to the lower surface. Percid percentage is then trapped on the lower surface, unless fishing intensity is substantially reduced, allowing the behavior to proceed back across the fold and jump again to the upper surface. That is, transitions between low and high percid percentages would be predictable at quite different values of the two control variables. It is particularly worthwhile to consider the management implications for a fishery that is started on a lake of intermediate MEI, say ln MEI = 2.5. In this instance, the fishery would, if intense enough, fall to the lower surface with no prospect of being returned to a high percid percentage by any further manipulation of fishing effort, including closure of the fishery.

Once looked at in this way, numerous potential examples of catastrophic community behavior come to mind: the alternating predominance of North Sea cod and haddock, or Gulf of St. Lawrence herring and mackerel, or California sardine and anchovy are but a few of the possibilities. Popova and Sytina (1977) and Bonar (1977) suggest similar examples for percids. Potential examples that are apparently suited to elementary catastrophe models are not hard to find; the trick (there is always a hard part) is to find tractable formulations for the underlying dynamics.

The present application to percid communities is necessarily preliminary and tentative, owing to the relatively few data that could be used in the model. In particular, evidence for the requisite bimodality is weak because of the many sources for heterogeneity in the available data. The model is offered now, in part because of the exciting possibilities it suggests for a theory of community structure and in part because of the important management implications it contains, if valid. Even in the oversimplified form provided here, there seems sufficient promise to justify further development of this approach as more extensive data become available.

Structure of Fish Production Systems

A useful means for depicting the structure of fish production systems is provided by the particle size-concentration distribution observed for marine pelagic systems by Sheldon et al. (1972). Despite a lack of suitable data, there is theoretical reason to believe that freshwater systems are characterizable by similar size distributions (Kerr 1974). A schematic example of the distribution is provided in Fig. 5.

The general picture of fish production systems that emerges from this representation is one of a general flow of materials and energy from the smaller to the larger particle sizes. The particular form of any observed distribution is primarily mediated by size-dependent predation and competitive displacements (Kerr 1974). Platt and Denman (1977) have used spectral analysis to derive a continuous model based upon these ideas.

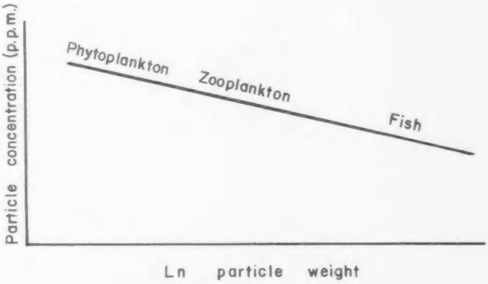

FIG. 5. Schematic representation of the pelagic size distribution described by Sheldon et al. (1972).

In the present paper, we have considered the possibility that modification of two basic control variables, fishing effort and lake productivity, serves to change the structure of the overall size distribution, through effects on community composition. There is preliminary evidence, provided above, that the induced community changes may at times be precipitous and that the permissible number of possible species combinations is rather more restricted than would result from simple mixing of continuous abundance gradients. That is, there is reason to suspect that a relatively small number of possible species combinations are reflected in the general size distribution.

At this juncture it may be helpful to make explicit connection between the size-dependent hypothesis and the percid frequency model of Fig. 3. The data analyzed for Fig. 3 reflect a number of fisheries for various species. Of these, only percids (mostly walleye) and coregonines (largely lake whitefish) are important and common in nearly all the lakes in the sample. A model identical to Fig. 3 can therefore be constructed by considering the ratio of percids to coregonids instead of the ratio of percids to total yield. That is, the model can be considered to represent the predominance of coregonid, as opposed to percid, communities. Owing to the average size differences between coregonids and large percids (walleye), which feed at different stations in the size spectrum, it is possible to construct a similar model based on size composition, a model that is thereby translated directly into the size-dependent terms of Fig. 5.

Viewing the general structure of Fig. 5 as an overall constraint that must be satisfied by the various components of the fish production system, it is possible to examine the combined effects of changes in the control variables. The general effect of a variety of external perturbations is to change the mean size in a system (Woodwell 1970). Specifically, the effect of a fishery is to erode the right-hand limb of the distribution, reducing the mean size. On the other hand, modifying lake productivity, by nutrient enrichment for example, would raise the intercept of the distribution by increasing primary production, but the resulting effect on the mean size in the system would depend on the level of enrichment.

These considerations are devoid of explicit typological content. But, as we suggested above in discussing Fig. 3, modification of the same two control variables may lead to catastrophic changes in species composition, themselves associated with body size, as critical levels of the control variables are passed. Accordingly, it is possible that the critical conjunctions of control variables at the catastrophe margins indicate regions where the connectedness of the system exceeds stable values (Kerr and Ryder 1977), leading to system collapse and reorganization. Reorganization, by this interpretation, would consist in new community compositions (different surfaces of the fold catastrophes), caused by changes in the size-dependent interaction processes between organisms, resulting in a new overall distribution of particle size and concentration.

Taken together, the ideas offered here add up to a rather abstruse picture, especially in the sparse outline offered, only parts of which are supported with hard data. But, in defense, it can also be said that the picture is internally consistent, exciting, and most important of all, subject in many ways to refutation by appropriate analysis of suitable data sets.

Thus, demonstrable absence in natural systems of bimodal species compositions (or multiple modalities, if larger portions of the size spectrum of a production system are considered) would, for example, refute the notion of typologically discrete communities separated by abrupt transition zones, especially if appropriate time series of data were examined. And, in the larger context, the absence of conservative, orderly changes in the size spectrum of a system, in response to impressed stress, would call the size-dependent structural hypothesis into question. By these and similar means, either some flesh can be added to the foregoing skeleton or the spectral nature of the bones can be revealed.

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PERCID INTERNATIONAL SYMPOSIUM (PERCIS)

Quetico Centre, Ontario, Canada Sept. 24–Oct. 5, 1976

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